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*Silurian
(Late Llandovery-Ludlow)
Atrypid Brachiopods*

from Gotland, Sweden, and the Welsh Borderlands, Great Britain

Paul Copper



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Front cover: A limestone bedding plane surface (micrite) with two shells of *Atrypa sowerbyi* Alexander, 1949, from the locality Hemse 1, upper Hemse beds, unit C, SE Gotland [Br106545]. One shell shows the inner part of the brachial valve with a frill attached, and the other shows the pedicle valve exterior, with most of the frills detached except the final frill. A digitate bryozoan skeleton is located next to the two atrypid shells.

Correct citation for this publication: Copper, P. 2004. *Silurian (Late Llandovery-Ludlow) Atrypid Brachiopods from Gotland, Sweden, and the Welsh Borderlands, Great Britain*. NRC Research Press, Ottawa, Ontario. 215 pp.

*A Publication of the
National Research Council of Canada
Monograph Publishing Program*

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Atrypid Brachiopods
from Gotland, Sweden, and
the Welsh Borderlands, Great Britain**

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NRC·CMRC
NRC Research Press
Ottawa 2004

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Printed in Canada on acid-free paper. 

ISBN 0-660-19011-7

NRC No. 46318

National Library of Canada cataloguing in publication data

Copper, Paul, 1940-

Silurian (Late Llandovery-Ludlow) Atrypid Brachiopods
from Gotland, Sweden, and the Welsh Borderlands, Great Britain

Issued by the National Research Council of Canada

Includes bibliographical references

ISBN 0-660-19011-7

1. Brachiopoda, Fossil - Sweden - Gotland.
2. Brachiopoda, Fossil - Wales.
3. Brachiopoda, Fossil - Great Britain.
4. Paleontology - Silurian.
- I. National Research Council Canada.
- II. Title.

QE796.C66 2004

564.68

C2003-980084-9

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Abstract

A rich and well-preserved atrypoid brachiopod fauna from the Silurian carbonate platform of Gotland (Sweden), in the Baltic Basin, and the siliciclastic-dominated ramp setting of the Welsh Borderlands in the Anglo-Welsh Basin, Britain, is assigned to three suborders (Anazygidina, Lissatrypidina, Atrypidina), four families (Atrypidae, Anazygidae, Lissatrypidae, Glassiidae), 13 genera, and 48 species. Sixteen new species are described. These span ca. 20 million years of evolution in the Atrypida at a critical stage in their early diversification, ranging from the late Llandovery (late Telychian, *crenulata* Zone) to late Ludlow (Ludfordian, Whitcliffian, *bohemicus* Zone). For more than two centuries, the Baltic and Anglo-Welsh basins have provided the source for many of the type species of well-established, key genera, including the founding genus and type species of the order Atrypida, *Atrypa reticularis* (Linnaeus, 1758). For the first time, the interior structure of the complete lophophore support, the brachidium (crura, spiralia, and jugal processes), is reconstructed for the genera *Atrypina*, *Oglupes*, *Plectatrypa*, *Spirigerina*, *Septatrypa*, and *Reticulatrypa*, as well as for other well-known as well as new species. Synonymies are clarified for several species-groups, and evolutionary trends in the succession of species are demonstrated for several genera, assisted by comparisons of infraspecific and interspecific variation within and between species. None of these trends demonstrate evolutionary stasis of long-lived species, not even the grab-bag species *Atrypa reticularis*, but instead record a constant flux, and commonly random, evolutionary spectrum of atrypid species and variation through the time

analysed for this region. Appearances of new genera were initiated either via immigration from the eastern tropics (e.g., *Atrypoides* from the eastern tropics), or evolution within the west European domain of Baltica. Transitional species occur in the *Gotatrypa*-*Atrypa*-*Oglupes*-*Endrea* complex, and the *Plectatrypa*-*Xanthea*-*Eospinatrypa* lineage, marking the arrival of spinose atrypines. Evaluation of the modes of life, and biogeographic distribution, shows that the atrypids occupied a range of benthic ecological niches, from deeper water, slope, and distal shelf or ramp to shallow, onshore oncoid, ooid, and carbonate sand to mud shoals, under more restricted conditions: none occupied the shallowest subtidal, or intertidal zones. A number of atrypids became reef dwellers for the first time, especially *Spirigerina*, *Xanthea*, and *Endrea*, although most taxa were off-reef, and a few were almost exclusively deeper water taxa. None of the distinctive Late Silurian atrypid fauna from the Urals appears to have been present, suggesting a partial block to migration during the Middle and Late Silurian, or unique Uralian reef niches absent in the Baltic. The upper Llandovery - upper Ludlow succession of NW Europe was marked by six benthic 'events' in the history of the atrypids: these are documented as radiations, declines, extinctions, and migrations of genera across the shelf area of the paleocontinent Baltica. These events coincided with reef expansions and declines, but did not coincide with those recorded for conodont and graptolite pelagic biota, suggesting that the tropical benthos was less perturbed by regional sea-surface changes, and was probably decoupled from the pelagic biota.

Résumé

Une faune diversifiée et bien préservée de brachiopodes atrypoides de la plate-forme carbonatée du Silurien de Gotland (Suède) dans le bassin de la Baltique et de la rampe siliciclastique de la Bordure galloise dans le bassin Anglo-Welsh (Grande-Bretagne) est regroupée dans trois sous-ordres (Anazygidina, Lissatrypidina et Atrypidina), quatre familles (Atrypidae, Anazygidae, Lissatrypidae et Glassiidae), 13 genres et 48 espèces, dont seize nouvelles. Elle couvre une période d'évolution d'environ 20 millions d'années chez Atrypida — une étape critique dans leur diversification initiale — s'étendant du Llandoveryen tardif (Télychien tardif, Zone *crenulata*) jusqu'au Ludlowien tardif (Ludfordien, Whiteliffien, Zone *bohemicus*). Depuis plus de deux siècles, le bassin de la Baltique et le bassin Anglo-Welsh ont été le lieu de découverte d'un nombre important d'espèces types et de genres clés, dont le genre fondateur et son espèce type, de l'ordre Atrypida, *Atrypa reticularis* (Linné, 1758). De plus, c'est la première fois qu'un « squelette » de soutien du lophophore, le brachidium (les crura, les spiralia, et les processus jugaux), est reconstitué pour les genres *Atrypina*, *Oglupes*, *Plectatrypa*, *Spirigerina*, *Septatrypa* et *Reticulatrypa*, ainsi que pour des nouvelles espèces et d'autres bien connues. Les synonymies sont précisées pour plusieurs groupes d'espèces et des tendances évolutives dans la succession des espèces sont décrites pour plusieurs genres à l'aide de comparaisons de variations infraspécifiques et interspécifiques. Aucune de ces tendances ne démontre l'existence de stases évolutives, et ce, autant chez les espèces dont la durée de vie est courte que chez l'espèce « fourre-tout » *Atrypa reticularis*. En fait, ces tendances indiquent plutôt des trajectoires évolutives qui changent continuellement et souvent de façon aléatoire chez les espèces atrypides ainsi que des variations dans l'échelle temporelle analysée pour cette région. L'apparition de nouveaux genres a été le résultat d'un phénomène d'immigra-

tion des régions tropicales de l'Est (p. ex. *Atrypoides*) ou d'un processus évolutif au sein du domaine européen de l'Ouest de Baltica. Des espèces transitoires ont été décelées dans l'ensemble *Gotatrypa*-*Atrypa*-*Oglupes*-*Endrea* et dans la lignée *Plectatrypa*-*Xanthea*-*Eospinatrypa*, soulignant l'arrivée des atrypines épineux. L'évaluation de leurs modes de vie et de leur distribution biogéographique révèle que les atrypides occupaient des niches écologiques benthiques variées — allant des eaux profondes, des pentes et des rampes et des plateaux distaux jusqu'aux hauts-fonds peu profonds de type oncoïde, ooïde et des hauts-fonds sablo-vaseux et carbonatés, sous des conditions plus restrictives : aucune espèce n'occupait les zones infratidales et intertidales. Un certain nombre d'atrypides ont occupé, pour la première fois, les milieux récifaux, surtout *Spirigerina*, *Xanthea* et *Endrea*, quoique la plupart des taxons se retrouvaient hors des récifs et quelques-uns vivaient exclusivement en eau profonde. On dénote également l'absence des espèces caractéristiques de la faune atrypide du Silurien tardif de l'Oural, ce qui suggère l'existence d'un obstacle partiel à la migration au cours du Silurien moyen et tardif ou l'absence de niches ouraliennes spécifiques dans le bassin de la Baltique. La succession du Llandoveryen supérieur — Ludlowien inférieur du Nord-Ouest de l'Europe a été marquée par six « événements » benthiques au cours de l'histoire des atrypides, soit par des périodes d'expansion, de déclin, d'extinction ou de migration des genres le long du plateau du palécontinent Baltica. Ces événements coïncidaient avec les expansions et les retraits des récifs, mais ne coïncidaient pas avec ceux notés pour le biote pélagique composé de graptolites et de conodontes, ce qui suggère que la faune benthique des régions tropicales ait été moins affectée par les changements locaux qui s'effectuaient à la surface de la mer et qu'elle ait été possiblement dissociée du biote pélagique.

Acknowledgments

Throughout all stages I have received encouragement from colleagues in Sweden, Britain, Estonia, and the Ukraine (Podolia), as well as Russia and China, and access to old and new type collections, assistance in the field, the loan or donation of extensive literature and reprints, translations from Swedish, and accommodation provided on Gotland, and at the Riksmuseet, Stockholm. For field work on Gotland in 1974, 1989, 1990, and 1995, particular thanks go to Valdar Jaanusson (Riksmuseet Stockholm), Sven Laufeld (Uppsala), and Lennart Jeppsson (Lund) for much helpful advice and data, Arne and Vivianne Philips (information about overflights), Lars Ramsköld (for translations, specimens, field advice), Doris Fredholm (field data, access to Allekvia), Colonel Lennart Ström (for access to restricted military areas, and accompaniment in the field), and Stellan Hedgren (for access to the nature preserve of Stora Karlsö). For Great Britain, my thanks go to Robin Cocks and Howard Brunton (Natural History Museum, London), Dennis White (Geological Survey), Stephanie Etchells-Butler and D. Price (Sedgwick Museum), and Madis Rubel (Academy of Sciences, Tallinn).

Mike Bassett (National Museum of Wales) provided me with the needed materials from Lilla Karlsö, and stratigraphic advice required for this revision. Patrick Racheboeuf (Université Bretagne Occidentale, Brest) provided me with stimulation through long discussions and advice while working on the Gotland monograph on one sabbatical leave in Brest. Robin Morrison and Laura Pearsall completed most of the photography, and the latter, in addition, carried out the SEM photography of sculptural details on the shell surface, as well as shell structure. My daughters, Pia and Lucina Copper, my son Quintin Copper, friend Angeli Mitra, and spouse, Karin Müller, accompanied and assisted me at various times in the field. Vincenzo Pascucci (Siena, Italy) and Reinhold Leinfelder and Martin Nose (Paläontologisches Museum, München) provided me with space, materials, and equipment to complete the revisions of the manuscript. The Natural Sciences and Engineering Research Council of Canada generously provided me with long-term financial support. The National Research Council of Canada, Ottawa, supplied editorial and publication assistance.

Introduction

During the Silurian, England, Wales, Scotland, southern Norway, and Gotland were part of the southwestern corner of the Baltica paleocontinent (the Anglo-Welsh Embayment, or Avalonia, was fused to Baltica at this time; Kiessling et al., 2002). The area lay in tropical latitudes approximately 20° south of the equator, about the same latitude as the centre of the Australian Great Barrier Reef is from the equator today. This ensured that warm tropical currents favoured the Baltica continental shelf areas, and that the reefal carbonate factory flourished in the Baltic Basin and Britain. This occurred at a time of global greenhouse warming and large-scale reef development, especially in the Wenlock (Copper, 1994, 1997b, 2002a). The seafloor community was rich in benthic life, i.e., photosynthetic producers (calcimicrobes, calcareous algae), and a range of invertebrate and vertebrate consumers. A relatively narrow sealane, the Iapetus Ocean, probably less than 600–1000 km wide, separated the Baltic Shield from the Laurentian Shield to the west at this time. Ocean current systems in the southern hemisphere followed a counter-clockwise gyre, thus moving waters along the southern equatorial latitudes towards the west, i.e., from the Podolian shelf towards the Baltic Basin and later to the Anglo-Welsh Basin (Fig. 1). About 1400 km separated the southern tip of Gotland from the nearest fossiliferous shelf area at Dudley and Wenlock Edge in the Anglo-Welsh Basin (a little less to the shelf deposits of Podolia), and the Anglo-Welsh Basin was firmly connected to Baltica at this time according to recent paleogeographic reconstructions (Golonka, 2002). Less than 100 km separated the eastern margins of Gotland from the nearest coeval outcrops in the eastern Baltic Basin of Estonia, Latvia, and Lithuania. The Prague Basin was part of another distal, smaller southwest European micro-plate, in the 40° south latitudes, either proximal to Gondwana (see Golonka, 2002), or an insular, mid-oceanic plate much closer to Baltica (Franke, 1999). There is considerable faunal similarity between the Baltic and Prague Silurian faunas, although Franke (1999) places another micro-plate, Saxo-Thuringia, between the Baltic and Prague basins. At the beginning of the Silurian (Llandovery, Rhuddanian), extensive shelf seas began to cover large areas of the Baltic paleocontinent, in partial response to global warming trends, and deglaciation in North Africa. But in the Aeronian, reefs re-appeared almost on a worldwide basis, and with them the first atrypids specialized towards reef settings (e.g., the East

Point reefs of Anticosti with *Dihelictera* and *Septatrypa*; Copper, 1995; Copper and Long, 1998; Copper, 2002a). Further reef specialization for atrypids occurred in late Telychian and Wenlock times in the reefs of northwestern Europe and Canada. By the end of Silurian time (Pridoli), however, Old Red Sandstone, terrestrial and siliciclastic shoreline facies had already spread progressively over the Baltic Shield from the north and west. This marked a retreat of the seas from the area, as a result of gradual closing of the Iapetus Ocean and the advancing Caledonian Orogeny (Laufeld and Bassett, 1981; Bassett, 1986).

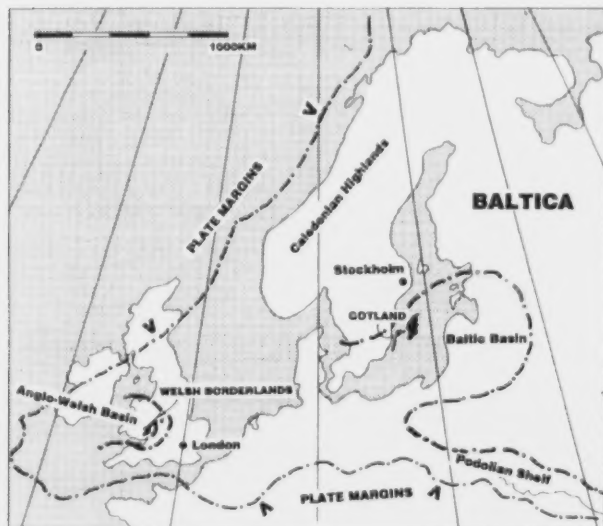
In this setting, a diverse and abundant benthic marine fauna and flora flourished, and reefs, from deeper water mudmounds to small patch reefs, then a larger, shallower shelf reef tract up to 1300 km long took hold, stretching from Podolia (Ukraine), through northern Estonia and Gotland, especially in Wenlock Ludlow time (Mantou, 1971; Riding, 1981; Zadoroshnaya et al., 1982; Ratcliffe, 1988; Copper and Brunton, 1991; Riding and Watts, 1991; Nestor, 1995; Copper, 1997b; Samtleben and Munnecke, 1999; Samtleben et al., 2000). Reef development in Britain, isolated to the west, was limited to the late Wenlock (Ratcliffe and Thomas, 1999). Active island arc volcanism at the western sides of Baltica, and tropical, monsoonal lateritic erosion of high-relief highlands to the centre and north (which intersected the equator), stimulated not only the sedimentation of ash falls (bentonites), but provided also a vast supply of siliciclastic clays, silts, and sands, especially in the Anglo-Welsh Basin (Bassett, 1986). Siliciclastics played only a minor role on Gotland, such as in the production of the Slite siltstones and Burgsvik sandstones. Gotland was a carbonate factory, largely bypassed by the flow of terrestrially derived material from the northwest. Such environments produced a large array of sediment types, highly variable substrates for the settlement of epibenthos and infauna, and a diverse suite of ecological niches. All this stimulated one particular group, the atrypid spire-bearers, which had first appeared in the late Middle Ordovician, to multiply, diversify, and frequently, to conquer and dominate the low-latitude shell-bed habitat, pushing out many other groups. This study is an attempt to describe the morphology, evolution, and paleoecology of the highly successful Silurian atrypid spire-bearers, amongst the most abundant shelly, pavement-forming animals of the time.

Techniques

The material from Gotland is superbly preserved, and diagenetically unaltered, as evidenced by SEM views of shell structures. The sequence is tectonically undisturbed, with no conodont colour alteration. Limestone and calcareous shale alternations with very early cementation show virtually no compaction, which have suggested to some that the primary material was aragonitic muds in the microspar range (Munnecke and Samtleben, 1996; Munnecke et al., 1997). Similar preservation is evident in the Anglo-Welsh material.

Nearly 13 000 atrypid specimens were measured for width, length, depth, height of the fold or sulcus, and, where applicable, rib density (calculated in ribs per 5 mm of arc along the anterior commissure) and spacing of concentric growth lamellae or filae. Following convention, in the text the pedicle valve is referred to as the ventral valve (vv) and the brachial valve as the dorsal valve (dv). The main characters used for description are outlined in Table 1, and these may be used for cladistic analysis.

Fig. 1. Location map of the Welsh Borderland (Anglo-Welsh Embayment) and Gotland (Baltic Basin), behind Byelorussian–Ukrainian (Podolian) shelf, as part of the Baltica paleocontinent. The British faunas are on the western outboard, part of the Anglo-Welsh embayment fused to the Baltic Plate by the middle Silurian (Kiessling et al., 2002), dominated by siliciclastics derived from the east and northeast. The paleo-plate margins of Baltica are only roughly defined. The Baltic Basin, including Gotland, Estonia, Latvia, and Lithuania, featured carbonate settings. The Baltic Basin is effectively an embayment that is an extension of the Byelorussian–Ukrainian shelf to the southeast.



Wherever possible, an attempt was made to rediscover the type locality. Such sites were re-examined, when they could be found, and fresh collections were made to establish population variation. Statistical comparisons were made of material from the type and other localities. Where a species was scarce, collections from several localities at the same stratigraphic level were pooled for statistical values. For very rare collections, statistical evaluation of size and shape was not possible. The general assumption, on which species descriptions were based, was that all specimens belonging to a single genus, from a single locality and horizon, could normally be assigned to the same species and that all variation was thus attributable to species variation. This corresponds to the concept of 'Binca tunggal ika', i.e., 'they are various, yet they are one' (from old Javanese, in the Sutasuma, a classic Indonesia myth, like the Ramayana, dated approximately 1365). Since most atrypoids examined were confined to specific milieus, e.g., peri-reefal facies (like the Höglint), or deeper water muddy facies (like the Mulde Marl), ecologic variability was not a major problem. Details of the external parts of the shell were sketched with a camera lucida mounted on a binocular microscope. Plaster casts were made of all specimens prior to sectioning, using Vinamold rubber compound. For internal views of the dorsal and ventral valves, loose shells were photographed, when available. Very large infraspecific variation in the size and shape of adductor and diductor muscle scars, vascular ca-

nals, and gonadal pits was evident, and a taxonomy based on these was not employed, for example, as in Boucot and Johnson (1964b) and Boucot et al. (1965). Very few shells were in siltstones or sandstones, and when present, were poorly preserved, and no silicified material was located: thus identifications were not based on internal or external moulds, except where unavoidable. About 50 shells collected were provided for stable isotope analyses (Azmy et al., 1998).

Internal structures of shells were studied primarily by serial sectioning to determine the nature of the delthyrial structures, teeth, crura, spiralia, and jugal processes. No previous data existed for Silurian shells from Gotland and the U.K., except for those published (Copper, 1997a, b, 1986, 1996b). For serial sectioning, specimens were coated with beeswax (to prevent etching of the shell sides by acids), then mounted in vertical position, lateral commissure upright, on stainless steel mounts, then fixed to the mount with beeswax. Serial sectioning was carried out with a Croft parallel grinder at 0.1 mm intervals for most shells, except very small shells (<5 mm width), which were polished at intervals of 0.05 mm with 600 grade carborundum powder. Peels were taken from each section by etching with weak (ca. 3%) hydrochloric acid, washing and drying the surface, then using acetone and pressing peels of Acetobutyrate Triafol MB (*TM Bayer A.G.) to the surface, letting the peel dry for 15 s, and carefully removing the peel from the polished surface. Peels were then examined under a petrographic microscope [photographed if required], and enlarged on paper using a slide projector, usually at a scale of $\times 20$ (for larger shells at $\times 16$). The outlines of the individual growth layers were sketched from the projected surface at specific intervals related to the development of the brachidia. Sectioning was normally halted at mid-shell, or at the peak of the spiral cones: time required for sectioning one specimen was usually between 16 and 20 hours. For reconstructions, two-dimensional diagrams were re-oriented into three dimensions in the plane of symmetry, and tracing all features carefully using a millimetre scale at $\times 20$ or $\times 16$. These reconstructions are accurate to 0.2 mm at a scale of $\times 1$. Use of this technique enabled the precise reconstruction of shell interiors for all species with spiralia preserved, nearly all for the first time. Serial sections were drawn on tracing paper with drawing ink, and reduced to a scale of $\times 5$ or $\times 4$. Shell surfaces were photographed using a Cambridge SEM 120 at Laurentian University. Other photography was carried out using conventional close-up photographic techniques, employing magnesium oxide coatings. The type and figured materials are deposited at the Natural History Museum (London), the Riksmuseet (Stockholm), the Sedgwick Museum (Cambridge), the British Geological Survey (Keyworth, Nottingham), the Holcroft Colln., Lapworth Museum (University of Birmingham), and the Linnean Colln. (Linnean Society, London). Additional materials, including serial peels and casts made prior to serial sectioning, are deposited at the Natural History Museum (London) and the Riksmuseet (Stockholm).

Table 1. Characters used in differentiating atrypid taxa. (*Prime characters*, used to differentiate genera, families, superfamilies, suborders.) [* = primitive, i.e., primitive character listed first; others are derived; characters multistate, gradational].

1. Orientation of spiralia = * medial, -dorsomedial, -dorsal
2. Number of spiral whorls = <1*, 1*- ~8, >8 whorls
3. Nature of jugum = * incomplete (partially formed), -complete
4. Nature of jugal processes = * dorsally, -medially or -ventrally located
5. = * anterior, -central, or -posteriorly located
6. = * small jugal plates, -complex jugal plates
7. Crura = * simple, thin, short, -feathered, long, thick
8. Shell wall, secondary layer = * thin, -thick, multi-layered
9. = * non-fenestrate, -fenestrate
10. Growth lamellae = * absent, -short, -long
11. = * single frill on margin, -multiple frills
12. = * parallel to shell surface, -oblique, -normal
13. = * equal length lamellae, longer on rib crests, longer in rib troughs
14. Ribs = * straight, one sequence, -overprinted by coarse ribs
15. = * expanding, coarse (non-bifurcated, intercalated) -continuous, fine (multiplying)
16. = * ribbed, -smooth
17. = * uninterrupted, -wave-like rows (interrupted by growth lamellae)
18. = * non-spinose crests, -spinose crests
19. Microornament = * absent (smooth), concentric filae, zigzag filae (primary layer)
20. = * absent, -capillose (secondary layer), -brush-like (primary layer)
21. Ventral beak = * small, -expanded, protruding
22. Hinge = * small, astrophic (curved), -large, strophic (flat)
23. Area = * orthocline, anacline, hypercline
24. = * orthocline, -apsacine, -procline
25. = * symmetric, -asymmetric
26. = * orthocline, -adpressed
27. Delthyrium = * small, -large
28. = * exposed, -covered (by hypercline, adpressed area)
29. = * small, -reduced, -absent (lost)
30. Foramen = * occupying all of delthyrium, -part of delthyrium
31. = * apical, -transapical
32. = * small, -large
33. = * small, -absent (lost by incurvature, or closure)
34. Deltidial plates = * absent, small, -prominent
35. = * small, -lost (resorbed)
36. Muscle scars = * small, -large
37. = * not impressed, -faintly impressed, -deeply incised
38. = * not impressed, -raised on secondary layer, -free platforms (septa)
39. Shape (convexity) = * ventribiconvex, -biconvex, -dorsibiconvex, -convexoplane
40. = * ventribiconvex, -planoconvex
41. = * weakly biconvex, -flat
42. = * weakly biconvex, -highly globose
43. Size = *small (<8 mm), medium (8-25 mm), large (>25 mm)
44. Outline = rounded, -shield-shaped, -triangulate, -elongate
45. Cross-section = rounded, -squared, -ellipsoid
46. Hinge-line = * short, -medium, -long
47. Hinge plate = * divided by cardinal pit, -flat, raised boss
48. = * without cardinal process, with small c. p., prominent c. p.
49. = * small inner socket ridges, -large, bulbous inner socket ridges
50. = * without socket ridges, -with socket ridges
51. Crural bases = * small, delicate, -large rounded
52. Pedicle callist = * absent, thin, -filling in most of cavity
53. = * separate, -fused with deltidial plates
54. = * full pedicle callist, -pedicle collar
55. Vascular canals = * absent, -strongly defined ridges
56. Gonadal pits = * absent, -strongly defined, deep
57. Anterior commissure = * sulcate, -rectimarginate, -plicate
58. Lateral commissure = straight*, curved, geniculate

Note: Atrypida lack a notothyrium, chilidium.

Historical background

The first description of an atrypid species from Gotland, albeit very brief and without any accompanying figures, dates back to Linnaeus in 1758, who named the species '*Anomia reticularis*' in his classic work, the *Systema Naturae* [see also Linnaeus, 1753, commonly cited; Davidson, 1866, p. 4, cites publication date as 1767]. This species subsequently became the type for the genus *Atrypa* (Dalman, 1828), and the name was used as characteristic for the whole order. Although the lectotype specimen of *A. reticularis* is preserved, and is herein figured, the precise type locality for the Linnaeus specimen is unknown (Brunton et al., 1967: the Linnaeus colln. in London contains several atrypides from different horizons on Gotland, encompassing more than one species). Most likely the type was collected from coastal outcrops near Hammaren in Östergarn Parish of eastern Gotland, where identical specimens occur (see under *Atrypa reticularis* description). Wahlenberg (1821, p. 65) cited the Linnaeus species from Gotland, but provided no figures. Dalman (1828) not only figured *Atrypa reticularis*, but also illustrated its ornament in detail for the first time. In 1828 Dalman also described and figured '*Atrypa aspera*', a species dating back to descriptions of a Middle Devonian form from the Eifel region by Schlotheim in 1813 [this Gotland species is re-identified as *Eospinatrypa hallae* n. sp. in this monograph]. Dalman added the smooth species '*Atrypa prunum*' [or *Atrypodea prunum*], and '*Terebratula marginalis*' [the type species of *Spirigerina*]. However, Dalman failed to notice the spiralia inside any of the dorsal valves in these species. Hisinger (1828) immediately cited Dalman's Gotland work, using the species figured as '*Atrypa prunum*', and later created another variety [now a valid species], *Atrypa reticularis* var. *alata* (Hisinger, 1831a). In 1837 Hisinger also re-figured the Dalman species *prunum* and *marginalis*.

In 1822 J. Sowerby described the first Silurian atrypid species, *Atrypa affinis*, from the Malverns and Dudley, England (although the specimen figured is a Devonian *Desquamatia*: see notes under *A. affinis* below). James de Carle Sowerby (1839) supplied the paleontological descriptions and figures of brachiopods for Murchison's classic 'The Silurian System', and illustrated seven new British species, *Terebratula tripartita* [= *Eospirigerina*], *Atrypa plana*, and *A. orbicularis* [= *Gotatrypa*] from Llandovery siliciclastics of Wales and the Welsh Borderland, and *Terebratula imbricata*, *T. imbricata* var. *abbreviata* (these are now two species assigned to the genus *Plectatrypa*), and *Atrypa subovata* and *A. compressa* [both = *Lissatrypa*] from Wenlock limestones and shales. J. de C. Sowerby (1839) used two different names, *Terebratula* and *Atrypa*, to describe his spire-bearers. Murchison (1847) described his trip to Gotland, collected faunas, and listed the atrypids under the contemporary names *Terebratula prisca* or *T. affinis* (the latter from Klinteberg, and correctly named for the species). Shortly afterwards, Davidson (1848) published his first Silurian atrypid species, *Terebratula barrandii* [= *Atrypina*] from the Wenlock [Dudley] Limestone at Walsall in Staffordshire, but did not use the genus name *Atrypa*. This paper was directly followed by a communication from Verneuil (1848), describing

new Gotland species of brachiopods, and a comparative list of species known to that date. In 1853 Davidson (pl. 7, figs. 89, 92, 93) began to adopt the name *Atrypa* and illustrated the dorsally directed spiralia of either Silurian or Devonian forms. Earlier, Blainville (1825, pl. 54, fig. 2a), DeFrance (1827, p. 295), and later von Buch (1840, pl. 33, fig. 8) had illustrated the dorsally pointed spiralia of Devonian atrypids belonging to the genus *Desquamatia*. The Devonian spiralia first figured by Blainville (1825) were only later discovered, described and figured in Silurian forms. Quenstedt (1852, 1867) used the term '*Terebratulae calcispirae*' for shells with dorsally directed spiralia, and later (Quenstedt, 1882) identified the atrypids as the family Procampyli, a name never adopted by others, and now abandoned. McCoy (1851) described the Welsh Llandovery species *Terebratula subundata* [= *Meifodia*], and the Wenlock form *Spondylobolus*, type *S. craniolaris*, as a new inarticulate genus. *Spondylobolus* refers to specimens assigned later to the smooth genus *Lissatrypa* Twenhofel (1914), and probably is a crushed specimen of *Lissatrypa obovata* (Sowerby, 1839: see Cocks, 1978). As first stated by Salter (1873, p. 135: see also Sedgwick, 1873, therein), *Spondylobolus* was 'a genus unfortunately founded in mistake': it became a nomen oblitum.

The second half of the 19th century saw the further description of Silurian atrypids from northwestern Europe, many from glacial erratic blocks transported southwards from or across the Baltic seafloor from Gotland, but some were described from bedrock. In 1861 Lindström added three new Gotland atrypid taxa, '*Spirigerina*' *imbricata* var. *lamellosa* [= type species of *Xanthea* Copper, 1996b], *Spirigerina marginalis* var. *costata* [= *Spirigerina costata*] and '*Spirigerina*' *sulcata* [= *Atrypodea sulcata*]. From specimens associated with glacial drift transported to north Germany from Gotland, Roemer (1861, pl. 5, fig. 13) illustrated *Terebratula marginalis* var. [= *Plectatrypa imbricata*]. Roemer (1862, p. 600) further noted '*Atrypa reticularis*' from glacial till in northern Germany. Because of their association with glacial drift, the derivation of many erratic fossils is not clear: a number may have come from Pridoli strata (the Beyrichien Kalk) exposed on the seafloor between Gotland and the southern shores of the Baltic (Martinsson, 1967: see also Krause, 1877). This was matched by Kunth (1865), who described a new smooth atrypid species, which he called *Atrypa laevigata*, from glacial erratics of northern Germany: for the first time, he showed the medially directed spiralia of the smooth genus *Glassia*. In 1865 Haswell described the late Llandovery species *Rhynchonella pentlandica* [= *Pentlandella*] from Scotland [refigured by Davidson in 1871: see also Boucot, 1964]. Davidson (1866) summarized the current work on Silurian brachiopods in Britain and Sweden, citing the pioneering work of Linnaeus and others [Davidson mentioned the publication date here for *Anomia reticularis* as 1767, and stated that the Linnaeus notes and manuscripts were located at the Linnean Society in London].

Richter (1866) added more species of Silurian atrypids from German glacial drift: these were *Spirigerina micula* [= ?*Reticulatrypa*] and *Rhynchonella succisa* [= *Septatrypa*], but the type materials have not been recovered. Roemer

(1866) simply listed Silurian taxa from Ilseburg in the Harz Mountains in Germany, e.g., *reticularis* and *marginalis* [not all references to other species listed herein by Roemer could be traced, e.g., to species cited as '*Atrypa socialis*' and '*A. marginiplicata*' by Giebel, 1858]. Davidson in 1867 reviewed most of the known Silurian atrypid species, and illustrated internal structures of several taxa. Krause (1877) also described (but did not figure) discoveries of *reticularis* and *imbricata* from the 'Beyrichien Kalk' in glacial till of northern Germany. Lindström (1880) described *Atrypa expansa* [= *Eospirigerina expansa*] from southern Sweden. Haupt (1878) added other, probably Gotland-derived, glacial erratic atrypid species, e.g., *Rhynchonella gallina* [= *Atrypina*], a species also described herein from upper Ludlow strata of south Gotland. In 1881 Davidson wrote two short papers, one citing the new Wenlock atrypid genus *Glassia* and the other a new species assigned to that genus, *G. elongata* (see under *Glassia*). Marr and Nicholson (1888) described the species, *Atrypa flexuosa* [= ?*Plectatrypa flexuosa*], from the Early Silurian Skelgill (Stockdale) Shales in northern England. Roemer (1885, pl. 9, fig. 21) added more glacial erratic species from the Baltic by describing *Rhynchonella trilobula* [= *Septatrypa*]. Some of the previously discovered erratic taxa were later cited and figured by Gagel (1890), although the lack of material prevents the proper re-description of many species described from glacial drift. From 1892 through 1895 Hall and Clarke summarized the contemporary status of many classic brachiopod genera, including those from Gotland and Britain. In 1899 Venyukov began to describe the Podolian shelf faunas, which, with further revisions in the following century, were to provide a better picture of the southeastern shelf along Baltica. Venyukov (1899) reported many of the classic European species from these Podolian sections, and added two new smooth species, '*Atrypa lindstroemi*' and '*A. sinuata*', which require revision because there are no internal data available (they are possibly rhynchonellids, e.g., *Plagiorhynchia*). Reed (1908) described '*Zygospira*' *haswelli* from latest Llandovery rocks of northern Britain, assignable to the catazyginiid genus *Pentlandella* Boucot (1964). Around the turn of the 20th century, at least 30 Silurian atrypid species had thus been described from the Baltic paleocontinent, and the attached Anglo-Welsh Embayment, i.e., the region stretching from Wales through England, southern Sweden, Gotland, northern Germany, and Podolia.

More recent work on northwest European brachiopods from the 20th century has seen a number of important revisions of older work, and the addition of new species and genera. In 1929 Kozłowski published his groundbreaking monograph on the Podolia (Ukraine) brachiopods, in which he established a number of new genera, among these Silurian *Atrypella* (= a junior synonym of *Atrypodea*), and *Septatrypa*. He used serial sectioning for the first time for these shells. Kozłowski's work on Podolian atrypids has subse-

quently been modified by Nikiforova (1954), Kulikov (1967), Modzalevskaya (1968), Tsegelnyuk (1976), Modzalevskaya and Nikiforova (1982), and Nikiforova et al. (1985). Struve (1966) revised some of the Gotland specimens on the basis of museum collections, and described a new subgenus, *Gotatrypa*, for specimens from the Lower Visby Formation. The Estonian brachiopods were studied by Rubel (1970; summary in Rubel and Roomusoks, 1970), who documented late Llandovery, deep-water *Pentlandella* there for the first time (sectioned in Copper, 1974), and described a new species of *Septatrypa*, *S. reclinis*. Worsley and Broadhurst (1975) selected a range of atrypid communities from the 14 million year long Early through middle Silurian interval of Norway, and lumped all the species under two names, *Protatrypa malmoeensis* and *Atrypa reticularis*; since none had photographic illustrations, their species may be assignable to several genera.

Following the work of Barrande (1847, 1879), extensive revisions and additions of the Prague Basin Silurian brachiopod faunas were carried out by Havlíček (1961, 1984, 1987a, b, 1990, 1991, 1998), Havlíček and Plodowski (1974), and Havlíček and Štorch (1990). These have added substantially to our knowledge of the European fauna. If Havlíček's species diversity numbers are correct, the Prague Basin is the world centre for atrypid species and genus diversity in the middle Paleozoic. This should be considered relatively anomalous, as the area covered by the Prague Basin is minuscule by comparison to Gotland, and preservation of much Bohemian material is fragmentary and poor, with internal structures unknown for most taxa. In addition, if paleogeographic reconstructions are correct (see Golonka, 2002), the Prague Basin is at almost 50° south latitude of the equator, at the margins of cold Gondwana, and this would be the only time in the nearly 100 myr evolutionary history of the Order Atrypida that they thrived at high latitudes. A similar problem exists with the Carnic Alps fauna (e.g., Gaertner, 1930), with many smooth Late Silurian atrypid taxa, e.g., *Septatrypa*, in common with those of the Prague Basin. Penn (1970; unpublished) considered '*Atrypa reticularis*' from the Welsh Borderlands and the Dudley-Birmingham area as containing 'successive geographical subspecies of a single chronospecies', based on statistical analyses of various forms from many horizons stretching from Llandovery through Ludlow rocks of Britain. Bassett and Cocks (1974) reviewed the more common brachiopod species from Gotland, assigning all ribbed Atrypinae broadly to *A. reticularis*, a system followed by Samtleben et al. (1996) and Wenzel and Joachimski (1996) for isotopic studies from Gotland materials. Copper (1977a, b, 1982, 1996b), revising primitive zygospirids, advanced lissatrypids, and ribbed atrypids, included a number of British and Gotland Silurian species and genera. Bassett (1979) studied the brachiopods of the Gotland Vattenfalllet section and described '*Septatrypa subaequalis*,'

Stratigraphic outline

The island of Gotland, about 140 km long and 55 km across (including Fårö and flanking islands), sits on the northwest edge of the Baltic Basin. Its ca. 445 m thick upper Llandovery through upper Ludlow outcrops of carbonates show almost continuous development of reefs and calcareous shales. These form a series of facies belts which strike roughly from NE to SW (Jaanusson, 1979), generally with the shallower parts of the section to the north and east, and deeper to the southwest. The richly fossiliferous strata contain suites of calcimicrobial stromatolites, coralline algae, stromatoporoids, tabulate and rugose corals, and a remarkable shelly benthos, which has been extensively collected and studied for about 250 years. Outcrops at the northern edge of the island start in rocks of late Llandovery age and end in the southwest with the youngest rocks being of late Ludlow age (Fig. 2). Late Telychian, Wenlock, and later shallowing during global periods of oscillating stillstands, with minor transgressions and regressions, produced a series of reef belts (Manten, 1971), and successions in extremely shallow water, with temporary emergence expressed in minor erosional hiatuses (Cherns, 1982, 1983; Calner and Jeppsson, 1999; Calner and Säll, 1999). Late Ludlow progradation of sediments added 'Old Red' sandstones, derived from a Caledonide highland to the northwest (Bassett, 1986; Bassett et al., 1989). The broad, as well as detailed, aspects of the stratigraphy of Gotland have been outlined in a series of geological papers accompanying map sheets which have provided the foundations for later work. Following early work by Hisinger (1827), Murchison (1847), Schmidt (1858), and Lindström (1888), there were a number of attempts to understand the relatively simple, slightly south-dipping sections, but complex facies relationships, ending with the comparison of Twenhofel (1916) prior to World War I. These were primarily the work of Hede and his colleagues during the 1920s to 1940s (e.g., Hede 1921, 1925, etc.). These studies are summarized in Hadding (1950) and Hede (1960), and reviewed, refined, and updated by Martinsson (1962, 1967), Laufeld (1974a, b), Jeppsson (1983), Riding and Watts (1991), Neumann and Kershaw (1991), amongst many others. More recent stratigraphic refinements include those of Jeppsson (1997a–c; 1998); Jeppsson and Männik (1993), Calner (1999a, b; 2000), Calner and Jeppsson (1999, 2002), Calner and Säll (1999), who added the Fröjel Formation; Jeppsson and Calner (2003); and Samtleben et al. (2000), with facies maps for the Wenlock–Ludlow interval. These provided the framework into which this study of atrypid brachiopods is inserted. Using the stable, low-Mg calcite shells of brachiopods, the Gotland section has been relatively well sampled for stable isotopes, e.g., Jux and Steuber (1992), Wenzel and Joachimski (1996), Munnecke and Samtleben (1996), Kaljo et al. (1997), Bickert et al. (1997), Azmy et al. (1998), and Samtleben et al. (1996, 2000). Such faunal and facies data are here incorporated and compared with the rest of the Baltic Basin, e.g., Estonia, Lithuania, and Latvia (Aaloe and Nestor, 1977; Nestor and Einasto, 1977; Kaljo, 1977, 1996; Kaljo and Klaamann, 1982a, b; Klaamann and Einasto, 1982; Kaljo et al., 1991; Nestor, 1997; Musteikis, 1991, 1993; Musteikis and Paskevicius, 1999), and compared with North

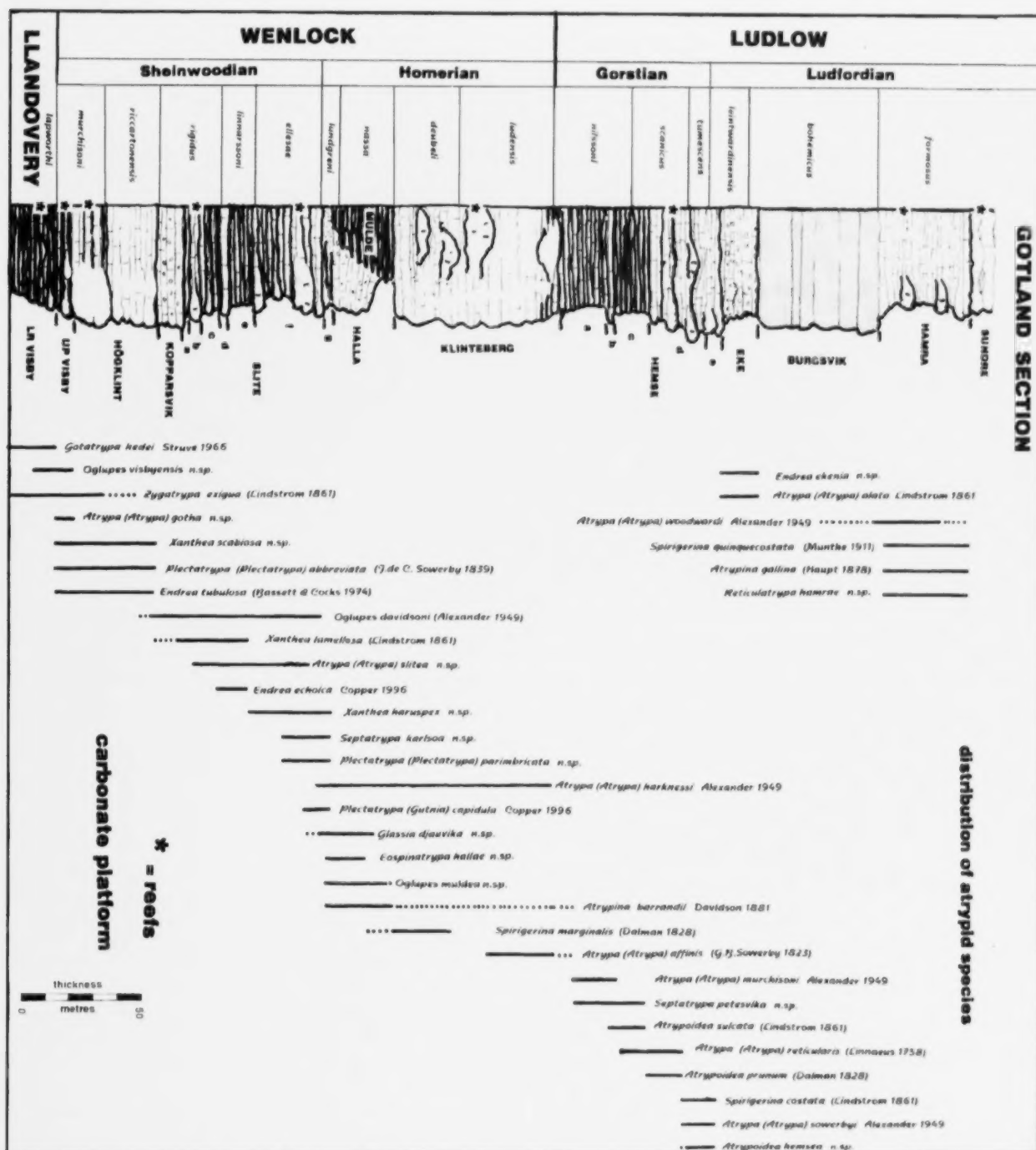
America (Saltzman, 2001). Bergström et al. (1992) have attempted to refine Baltic stratigraphy using K-bentonites tied into conodont zones.

In Britain, fossiliferous, benthic brachiopod communities of late Llandovery through Ludlow strata range from the southerly inliers of the Welsh Borderland northwards for about 100 km to Dudley and Walsall, and about 100 km westwards into Wales. The Silurian here was first explored in detail by Murchison (1833, 1839), with the fossils described by J. de C. Sowerby (1839). These span a slightly wider region than that of Gotland, including palinspastic reconstructions to remove tectonic folding and faulting. The late Llandovery through Ludlow succession in the Welsh Borderland region, in the area around Wenlock Edge, is about 600–750 m thick, thus about 30% thicker than the comparable section on Gotland (Fig. 3; e.g., see Ziegler et al., 1974; Cocks et al., 1971, 1992; Bassett, 1974, 1976; Holland, 1985). This suggests a strong and continuous input of siliciclastics into the Anglo-Welsh Basin from the land area to the north and east, and more rapid rates of sedimentation in the shelf margin, shelf break, and basinal successions. This affected the production of carbonates here, which became common only in Wenlock time (especially the late Wenlock, with patch reefs, and partial reef development in the lower Ludlow Aymestry limestones; see summary in Siveter et al., 1989). The significance of declining carbonate production during the Ludlow transgression was probably related to a new pulse of siliciclastic muds and silts, eliminating and smothering reef development. The normal marine sequence terminated in the Pridolian (Ludlow 'bone beds') with the advance of Old Red siliciclastics filling the Anglo-Welsh Basin, and the emergence of land area (the Pridolian–Devonian 'Old Red Continent'), where earlier there were shelf seas. Golonka (2002) showed that Avalonia and the Anglo-Welsh Basin were sutured to Baltica by middle Silurian time; faunal communications along the eastern shelf margins were thus well established. Comparable brachiopod faunas in the Prague Basin (Havlíček, 1961, etc.) suggest, however, that this region, as well as the area of the Harz Mountains, were not on the Gondwana margins, but probably on a terrane proximal to Baltica, or in an island arc setting, as volcanism was prevalent there (Kříž, 1991, 1998). Cocks and Fortey (1988), however, showed late Llandovery locations of the Prague Basin (Bohemia) and the Ukraine on the northern margins of Gondwana.

Stratigraphic distribution of atrypids in Gotland and Britain

Silurian strata of northwestern Europe, especially Gotland and Britain, contain a well-preserved, diverse, and relatively rich fauna of atrypids, many of which are the classic type species of well-known genera (Fig. 2). The ranges and distribution of these in the past have often been misconstrued or oversimplified. A number of atrypids have been identified correctly, and others misidentified on the basis of external form only, from the sequence in both Gotland and Britain.

Fig. 2. Distribution of atrypid species, Gotland, shown as species succession with time, in Gotland and the Welsh Borderland. Stratigraphic column of Gotland based on Hede (1960), and Laufeld and Jeppsson (1976), with species jointly found on Gotland and in Britain, shown adjacent to column: diachroneity of some higher units is partly omitted here. Note that diversity peaked in the late Wenlock. The thickness of the Gotland Wenlock-Ludlow sequence is ca. 445 m versus ca. 200 m for the more condensed shelf section of Estonia.



For example, the smooth genus *Lissatrypa*, part of the deeper water, muddy bottom, benthic assemblage (BA-5) in both Britain and the Baltic Basin, has commonly been labeled as "*Glassia*", which has very different medially oriented spiralia and distinctive cardinalia. The ribbed species *Atrypa reticularis* has been said to be present in strata from Llandovery through Ludlow age: its true age is restricted to the lower-middle Ludlow. Penn (1970) and Bassett and Cocks (1974) stated that they had discovered the Devonian genera *Desquamatia*, *Spinatrypa*, and *Spinatrypina* in Silurian rocks of Gotland, but no trace of these could be found in any collections examined. Some *Atrypoides*, e.g., *A. sulcata* and *A. hemsea*, were mistaken for *Lissatrypa* (Bassett and Cocks, 1974; Watkins, 1975). Some rhynchonellids, e.g., "*Septatrypa*" *subaequalis* Bassett 1979, were said to be atrypids. *Plectatrypa* have commonly been misidentified as *Spirigerina*. Here the various species discovered are examined in stratigraphic succession, with the type species preceding the list for each genus, where applicable. The distribution of atrypids in Gotland and Britain is interpreted in the light of the more fossiliferous Gotland section (Fig. 2). Rubel et al. (1991) documented a broad decline in diversity of brachiopods in the Wenlock section of Estonia: this is matched in the decline of Wenlock atrypids, with a maximum in the late Sheinwoodian and fall by the end Homerian.

The upper Llandovery-Ludlow succession of atrypid spire-bearers in northwestern Europe is marked by several evolution, immigration, extinction, and emigration events. A number of migrant taxa reached Gotland, but never made it as far as Britain, possibly because of facies constraints. The 'atrypid events' are the following:

- (1) The late Llandovery (Telychian) and earliest Wenlock marked the disappearance and (or) decline of the biconvex, unfrilled genus *Gotatrypa*, the loss of the last Anazygidae, e.g., *Pentlandella* and *Zygatrypa*, and the introduction and rise of the convexoplane, frilled genus *Atrypa*. The genus *Lissatrypa* marked the British Lower and middle Silurian sequence, but did not settle in the Gotland area. Small patch reefs appeared in the late Llandovery of Gotland, but none in Britain.
- (2) The dawn of the Wenlock (*centrifugus* Zone) saw the expansion of the first true small-shelled *Plectatrypa*, the appearance of exotic new, rapidly evolving taxa such as *Endrea* and *Xanthea*, and the rise of *Atrypina*, which were still insignificant in the late Llandovery, as well as the coming domination of frilly *Atrypa*. Reefs flourished in Gotland from the Upper Visby, through Högkling, Slite, and Klinteberg beds.
- (3) The Wenlock (Homerian) upper *ellesae-nassa* zones saw the invasion of the smooth atrypoids *Septatrypa* and *Glassia*, the former only in Gotland, the latter in both Gotland and Britain: the sudden appearance and origin of these taxa in NW Europe remains unclear (as their ancestors occur in the Early Silurian elsewhere). The first *Eospinatrypa* arise here, clearly endemically derived from their ancestral genus *Xanthea*.
- (4) The ribbed, reef-dwelling genus *Spirigerina*, e.g., *S. marginalis*, arrived in Gotland during the late Wenlock *nassa* phase, but did not apparently reach Britain until *ludensis* time. It evolved rapidly during the Ludlow. Reef habitats were introduced to Britain only during

ludensis time, accompanied by a burst in atrypid diversity, and introduction of taxa, probably from Gotland or Podolia to the east. There was no extinction of atrypid genera at the end of Wenlock time. In fact, worldwide there was a modest increase of two genera, and common Llandovery taxa died out or declined earlier in the Wenlock (e.g., *Gotatrypa*).

- (5) The *Atrypoides* lineage immigrated to Gotland from the east (probably originally from South China) during the early Ludlow *nilssoni* Zone, marking the introduction of an abundant, rapidly evolving new community which came to dominate much of Ludlow and Pridoli time, especially in nearshore, sheltered carbonate habitats. *Atrypoides* did not reach Britain, where siliciclastics dominated: some of these adapted to reef habitats. The genus *Atrypa* expanded, with great abundance, often excluding other taxa, and reducing diversity of other species.
- (6) The final phase, the Ludfordian, marked the decline or retreat of most atrypid stocks, with only reef and peri-reefal atrypids surviving in the region. One genus was introduced for the first time, the very finely ribbed form *Reticulatrypa*. Other stocks, such as *Endrea* and *Eospinatrypa* had already faded during the Ludlow, making only sporadic rare appearances, except locally. Reefs declined at the same time.

Lower Visby Formation (Ygne Member – late Llandovery)

Within the Lower Visby beds (Telychian), about 20 m of which are exposed, patch reefs are scarce, and those examined at Ireviken showed primarily a population of brachiopods, including strophomenids and rhynchonellids, in or near coral thickets. The most common atrypid brachiopods in the Lower Visby units are *Gotatrypa hedei*, *Oglupes visbyensis*, and *Zygatrypa exigua*, taxa that may sometimes be quite abundant in the very soft-weathering, blue-grey, clay shales that outcrop between beach boulders in areas from Gnisvård northwesterly to Ireviken. The first of these species occurs only in the Lower Visby units, but the others range upwards into the higher Visby beds. *Plectatrypa abbreviata* occurs in the peri-reefal and inter-reefal strata of the upper Lower Visby beds, its range extending into the Upper Visby beds. In the Lower Visby beds, Stel (1978, p. 9-10) illustrated some Ireviken biostromes and reefs, mentioning the presence of "*Atrypa reticularis*" (= ?*Oglupes visbyensis*). In Britain the uppermost Llandovery (Telychian) siliciclastic succession of shales, siltstones, and sandstones sees the presence of *Gotatrypa orbicularis* (no *Gotatrypa hedei* have been observed in Britain), *Lissatrypa* cf. *minuta* (not recorded in Gotland), and *Pentlandella haswelli* (not known in Gotland, but *Zygatrypa* is absent in Britain). Watkins et al. (2000) identified *Lissatrypa* cf. *minuta* as "*Glassia*" in their deep water *Clorinda* assemblage BA-5 from Britain.

Upper Visby Formation (Rövar Lilja Member – Wenlock)

The Llandovery-Wenlock boundary occurs somewhere either at the base of the Rövar Lilja Member or a few metres above the base (Laufeld and Jeppsson, 1976; Riding and Watts, 1991). The member is about 8.5–11.5 m thick (Jepp-

sson et al., 1994), and includes increasingly more reefal strata (the Axelro reefs) towards the top. In terms of atrypids, *Gotatrypa visbyensis* and *Zygatrypa exigua* continue from the underlying member into the Upper Visby strata. Somewhere above the base of the upper unit, particularly marked with the appearance of the Axelro patch reefs, is the introduction of new taxa such as *Endrea tubulosa* and *Xanthea scabiosa*, the harbingers of the Wenlock fauna. Atrypids occur in the reef and peri-reefal flanks of this unit, and these show differences from the preceding deeper water Lower Visby strata. Samtleben et al. (1996) and Samtleben and Munneke (1999) indicated a slight +ve shift in both δO^{18} and δC^{13} signatures at the boundary between the Lower and Upper Visby beds, preceding the arrival of upper Axelro patch reefs. Saltzman (2001) measured +ve δC^{13} excursions for the Nevada and Oklahoma sections in the U.S. at about this level.

Höglint Formation

Hedström (1923, p. 21), and later Munthe et al. (1927a, p. 51) cited the occurrence of '*Atrypa reticularis* var. *concentrica*' from the 35 m thick Höglint limestones, but this species has never been described, nor figured, and because it is unidentifiable in collections, it becomes a nomen nudum. Bassett (1979) cited the occurrence of *Atrypa* sp., *Eospinatrypa* sp., *Endrea tubulosa* (Bassett and Cocks, 1974), *Xanthea lamellosa* (= *X. scabiosa* n. sp.), *Plectatrypa* [= *P. abbreviata* (Sowerby, 1839)], and *Lissatrypa obovata* (Sowerby, 1839) in the Höglint beds from the Vattenfallet section near Visby (*Lissatrypa* could not be corroborated: specimens examined were athyrids). Most of these range upwards from the underlying Upper Visby beds, i.e., the Rövar Lilja Member. These atrypids were found within the Höglint patch reefs, either as reefal or perireefal taxa, e.g., *Xanthea* and *Endrea*. From the Korpklint reef-dwelling brachiopods, Watkins (2000) identified *Endrea tubulosa* as *Spinatrypa*, and *Xanthea lamellosa* as *Plectatrypa*. Sedimentation in and around the Höglint patch reefs was studied by Watts (1988): he looked at the skeletal reef frame-builders, the calcareous cyanobacteria, red algae, stromatoporoids, and corals, but omitted the epifaunal brachiopods. Riding and Watts (1991) further subdivided the Höglint beds into finer lithostratigraphic units, including patch reef units and inter-reefal strata, but did not discuss the distribution of brachiopods in these units.

Kopparsvik Formation (Tofta Kalksten)

Hedström (1910) mentioned the occurrence of '*Atrypa lamellosa*' [= *Xanthea scabiosa*] and other brachiopods from the *Spongostroma-Leperditia* beds, i.e., Tofta limestones around Visby. Hede (1960, p. 55–56) accentuated the low-diversity nature of the Tofta Limestone by citing only the occurrence of stromatoporoids, smooth leperditids, the red alga *Solenopora*, and calcimicrobe '*Spongostroma*'. In terms of atrypids, collections do not mention the 8 m thick Tofta beds as the source. However, it is very difficult to collect whole shells in the Tofta beds, some shells may be reworked from the Höglint beds underneath, and moreover, old collections often lack the precise stratigraphic information available to decide what faunas occurred here. To the northeast, this for-

mation is said to pinch out, but the patch reefs of the lower Slite beds, which occur on the north side of Fårö may correspond stratigraphically to the Tofta limestones to the southwest. If this is correct, the Tofta may be reefal in the NE, and brachiopods assigned here to the lower part of the Slite beds, e.g., *Xanthea lamellosa* and *Endrea echoica*, may be of Tofta age. A clue here may lie in the presence of these two brachiopods: the type locality of *Endrea echoica* at Endre, near Visby, and other citations of this species around Stenkumla (Martille), from the 'Slite beds', which may be mapped locally as Tofta lithology.

Watts (1988) first defined the Kopparsvik Formation in studying the sedimentation of the underlying Höglint reefs. Riding and Watts (1991) did not discuss the faunas of the Kopparsvik Formation, which they define as a ca. 7 m thick suite of biostromal, oncoidal to rubbly calcarenites overlying the Höglint strata, but they indicated that this thin unit is replete with disconformities and erosional gaps. Watkins (1992) suggested that the Tofta beds, including the patch reefs developed therein, formed in a protected 'intertidal, back-barrier' setting, but not in an environment with hypersaline or metahaline conditions, although an intertidal setting seems unlikely for atrypid brachiopods. He mentioned the occurrence of abundant stromatoporoids, oncoids, and a low-diversity brachiopod fauna, e.g., '*Septatrypa*', but no other brachiopods or atrypids. The brachiopod described by Bassett (1979) from the upper Höglint strata as *Septatrypa subaequalis* is a species of *Plagiorhynchia*, and the Tofta specimens of Watkins (1992) are assumed to be identical. Rhynchonellids are not unknown in intertidal settings, and there is no direct sedimentological evidence for an intertidal regime in the Tofta lithology, such as mudcracks.

Slite and Fröjel formations

The Slite beds are up to about 70 m thick (Hede, 1925, 1960; Jeppsson, 1983), and are composed of calcareous shales ('marls' of others), limestones (micrites, grainstones), and reefal limestones, with minor siltstones near the top. Munthe, Hede, and Lundqvist (1936) described units 'A' to 'F' as being about 28.5 m thick on the Fårö map sheet, with unit G up to 30 m thick, particularly thickened by local reefal units which are identifiable by polygonal jointing structures in the overlying strata that buried the reefs (Laufeld et al., 1978). The lowermost Slite on Fårö Island, unit 'A', up to about 4 m thick, contains 'sporadically very small bioherms' (Hede, 1960, p. 49; Watts and Riding, 2000), with the reefs developing a distinctive atrypid fauna consisting of *Xanthea lamellosa* (Lindström, 1861) and *Endrea echoica*, possibly age equivalent to the reefal Tofta Limestone below. The middle to high Slite beds of the NE contain an abundant *Atrypa slitea* fauna. The uppermost Slite reefal unit 'G' (Ryssnäs Limestone) of the NE facies contains a different *Xanthea haruspex* and *Gutnia capidula* fauna, and was said to lie in the *rigidus* graptolite Zone (Laufeld et al., 1978). According to Laufeld and Jeppsson (1976), the Slite and Fröjel beds span the *Cyrtograptus rigidus* to *lundgreni* graptolite zones. Jeppsson (1990) identified the uppermost Slite beds within the alleged 'arid' Hellvi Secundo episode, following the 'Valleviken Event'. Samtleben et al. (2000) placed the upper Slite beds, on the basis of sta-

ble isotope studies, in an 'H-period', a humid phase with estuarine circulation and eutrophic surface waters, terminated by a sharp isotopic change and shift to a dry 'A-period', of antiestuarine circulation and oligotrophic surface waters, marked by disconformities, and sandstones. In the upper Slite beds they indicated a reefal facies on the NE coast (i.e., the Ryssnäs facies), a dominantly proximal shelf facies in the centre, with deeper waters on the west coast towards Gannarveskär 1. Samtleben and Munnecke (1999) also analysed reefs in the Slite strata. The shaly units within the middle to high Slite strata (Bergman, 1980) are dominated by an *Atrypa (Atrypa) slitea* fauna, a locally abundant species with coarse, flat ribs and relatively wide frills. Smooth atrypids do not appear to be common in this shaly central and northern facies. In the uppermost Slite reefal facies around Tjälbersholm, small *Plectatrypa (Gutmia)* are present in patch reefs.

The topmost 10–11 m of the Slite Formation have been separated as the Fröjel Formation by Calner (1999a), with two units, the Svarvare and Gannarve members, defined on the SW coast. These were suggested to correlate with a relative sea-level fall. In the SW facies belt, as seen in strata on Stora Karlsö, there are biostromal beds rich in phaceloid and solitary rugosans in the high, but off-reef, deeper water Slite beds. These have a very different fauna consisting of *Plectatrypa parimbricata* and *Septatrypa karlsoa*, which tend to be rare to common in the biostromal coral beds, and probably represent species attached to corals in the coral thickets which occupied the seafloor in this region. *Oglupus davidsoni* occurs just below this biostromal setting in probably even deeper waters. Slightly to the north at Utholmen, *Atrypina harrandii*, a British species, makes a rare appearance. In the upper levels of the Slite beds, *Atrypa (Atrypa) harknessi* forms a small component in the local fauna on the SW coast in deeper facies. Several localities on the west coast, in the Klinte and Klintehamn parishes, south of Klintehamn (e.g., Svarvare, Odvalds, Sickling), have been identified as deeper facies 'Slite shales'. *Glassia djaupvika* is locally abundant in these shales, which give these very much the 'flavour' of the Mulde beds around Djaupvik.

The Fröjel Formation lies within the upper *lundgreni* Zone (Calner, 1999a), and was divided into the lower Svarvare and upper Gannarve members by Jeppsson and Calner (2002). The Fröjel Formation, said to define a middle to late Wenlock regressive phase and sea-level lowstand within the *lundgreni* Zone (Laufeld et al., 1978; Calner, 1999b), is marked by shallowing upward reef growth in the NE part of Gotland, and the deposition of siltstones or carbonate grainstones. The elastic end of this phase, which locally may have covered the reefs, terminated reef growth; some reef tops were eroded to the northeast, and locally a disconformity and hiatus mark sea-level drawdown during the mid-Homerian (Calner and Jeppsson, 1999). This break at the top of the *Cyrtograptus lundgreni* Zone is said to mark a global graptolite extinction event (Jaeger, 1991). Calner (2002) recorded a lowstand epikarstic surface at the top of the Fröjel Formation near Klintehamn. No major atrypid generic break, or phase of innovation, is evident at this horizon except for the loss of four species and the arrival of four new species, which coincides with a facies break (see Fig. 2). Jeppsson and Calner (2002) described the beginnings of the 'Mulde

secundo-secundo' event (spanning their Svarvare through Gannarve members), which was suggested to coincide with a brief glacially induced sea-level fall (the Gannarve glaciation), marked by severe loss of plankton productivity and zooplankton starvation. Conodont and graptolite extinctions were said to be most prominent in their lower units in Datums 1, 1.5, and 2.

Halla Formation

These upper Homerian strata are oolitic-oncolitic carbonate grainstones and packstones up to about 15 m thick, capping the Slite beds, and exposed in the central to NE facies of Gotland. These strata represent high-energy, unstable, coarse-grained, carbonate shoals, said to succeed a regression and unconformity marking the top of the Fröjel Fm. (Calner, 2000; Calner and Säll, 1999). Jeppsson and Calner (2002) recognized a Bara oolite member and coeval Hörsne reefal member for the Halla Fm. The oolites carry an exclusive fauna consisting of *Eospinatrypa hallae*, one of the oldest global occurrences known for a spinatrypinid, and no other atrypids. No atrypid fauna for the reefal Hörsne Member was available to me. A NE patch reef belt in the north-east facies belt (termed the Hörsne Member by Calner, 2000), with reefs, developed for a distance of about 15 km (but no atrypid fauna collected), succeeds the Bara oolites. On Stora Karlsö, and inland on Gotland, the equivalent strata are apparently also developed as reefal facies, but no atrypid fauna is available from either area. Their age is usually assigned to the *nassa* Zone, i.e., time equivalent to the muddy western Mulde facies. The presence of Halla oolites and pisolites, along with coeval Mulde beds, are said to mark a regional A-period, or arid climates and more oligotrophic conditions (Bickert et al., 1997; Samtleben et al., 2000).

Mulde Formation

The Mulde calcareous shales, which lie primarily, and possibly exclusively, within the *nassa* Zone, are generally recognized, at least for lower levels, as the deeper water time equivalents of the Halla oolites in part (Munthe et al., 1927b). Rich faunas have been collected there for more than a century from the spill heaps of the brick quarries, with the basal Mulde Brick Clay Mbr. overlain by the Djupvik Mbr. (Calner and Jeppsson, 2002; Jeppsson and Calner, 2003). The Mulde has also been viewed stratigraphically as a shaly member in the Halla Formation, e.g., as more recently in the description of western facies, tabulate coral biostromes by Calner et al. (2000). They viewed the coral thickets at the Blåhäll 1 locality as a signal of the only deeper water coral facies of the Gotland section (this would have to exclude the *Dokophyllum* biostromes of Stora Karlsö Island, and similar cup coral biostromes in the Lower Visby beds). To the southwest they overlie Slite Siltstones, apparently without a break. The soft weathering, lower to middle parts of the ca. 25 m thick Mulde marls, the Mulde Brick Clay Member, are especially rich in a monotypic atrypid fauna of *Oglupus muldea*. This species occurs only in the Mulde Marls on Gotland; this makes it difficult to correlate with other shallower facies of the Gotland section, e.g., the Halla beds. However, this is a species also known from the Farley Mem-

ber of the Coalbrookdale Formation [= Tickwood beds], also occurring in the *nassa* Zone there. True *Atrypa* are absent in the Mulde Marl. It may be possible that the Mulde Marls are in part time-equivalent to the Stora Karlsö reefal facies, continuing into the Klinteberg reefal facies, with the Mulde thus representing a deeper water, off-reef basinal facies of the Halla and also Klinteberg formations. The question remains if the Mulde may span not only the *nassa* but also part of the *ludensis* Zone. Higher in the Mulde beds (about the middle) are strata which locally carry a rich *Glassia djaurvika* fauna, a species also identified from 'Slite' beds around Västergarn. *Glassia* is absent from Klinteberg and higher strata on Gotland, although in the Prague Basin this genus occurs in rocks as young as the Pridoli. No atrypoid taxa became extinct within the *nassa* Zone equivalents on either the Gotland, or British carbonate platform and distal ramp. Indeed, this marks the introduction of *Eospinatrypa* in Gotland. In westerly areas where the Klinteberg platform and reefal carbonates are absent, there is no marked lithologic distinction between the uppermost Mulde and lower 'Hemse'-type facies, except that the former is more shaly and softer weathering (see discussion under Klinteberg Fm.). A negative δC^{13} excursion is said to mark the *nassa* levels in Britain (Corfield et al., 1992), in contrast to a moderate positive δC^{13} and weaker δO^{18} positive isotopic excursion that is said to mark the upper Homerian Mulde brachiopod shells (Azmy et al., 1998; Samtleben et al., 2000).

In Estonia, the Wenlock–Ludlow boundary in the platform Ohesaare section shows a slight +ve δC^{13} excursion, and a shift from dolostone to limestone, but at Priekule in Latvia no δC^{13} excursion is evident in the deeper water shale facies (Kaljo et al., 1997). In the Prague Basin, late Wenlock deep water calcareous shales show the presence of purported '*Glassia*', associated with graptolites and sunken nautiloids (Turek, 1983). This is somewhat similar to the deeper water occurrence of *Glassia* in the Mulde Marl of Gotland, but *Lissatrypa* is also known to be a deeper water inhabitant in many localities.

Klinteberg Formation

The mostly upper Homerian Klinteberg Formation is locally more than 70 m thick, consisting primarily of crinoidal-oncolitic grainstones and local patch reefs, deposited in very shallow waters in the west and central belt, with shoals and back-reef flats to the northeast (Jeppsson, 1983; Frykman, 1989). Reefs occur mostly in the southwestern facies belt. The upper 30 m of the Klinteberg Formation is said to span the Wenlock–Ludlow (W–L) boundary diachronously in the Wenlock *ludensis* through lower Ludlovian *nilssoni* zones (Jaeger, 1991; Jeppsson, 1983; Frykman, 1989). The lower Klinteberg boundary probably lies within the upper *nassa* or *deubeli* zones. The Klinteberg diachroneity, from the NE to SW, was first indicated by Martinsson (1967), on the basis of ostracodes. There appears to be no dramatic lithologic or faunal transition within the Klinteberg Formation to suggest a major facies change at the Wenlock–Ludlow boundary (Frykman, 1986; Calner, 1999b), similar to that expressed in England at Wenlock Edge. It has a moderate diversity atrypid fauna consisting of *Spirigerina marginalis* (Dalman, 1828) towards the base of the Klinteberg Fm., with rare *Atrypa*

affinis (Sowerby, 1823) near the top. The British late Wenlock species, *Spirigerina lockwenia* n. sp., does not appear on Gotland, and cannot be used to define the age of the uppermost Klinteberg strata. In deeper water facies of the southwest, *A. harknessi* is present. Precise subdivision of the Klinteberg using atrypid brachiopods does not seem possible, largely because new outcrops are not available; a calcimicrobial-stromatoporoid-coral assemblage dominates, brachiopods are scarce, and old collections do not define the precise collecting horizon. Back-reef Klinteberg facies have produced no atrypids for this study. The typical atrypid genus for the Klinteberg is the genus *Spirigerina*, with probably the lower part of the Klinteberg reefal facies supplying *Spirigerina marginalis*. This means that this species probably can be dated as belonging to the lower *ludensis* graptolite Zone. Frykman (1989), in a lithostratigraphic study of the Klinteberg, cited the "Klinteberget 1" locality with a basal packstone to grainstone overlain by three reefal members (B, C, and D); he did not cite occurrences of brachiopods. The reefal Klinteberg outlier on Lilla Karlsö Island contains *Spirigerina marginalis* identical to those seen from localities labeled 'Klinteberg' (specimens supplied by M.G. Bassett). Hurst (1975c), in his analysis of the Gotland communities, identified *Spirigerina marginalis* from his units G12–G13, in the basal 2–3 m of the Klinteberg beds, second only to *Conchidium* in abundance. Interbedded calcareous shales and micrites of the Snoder area, south of Mulde, contain a fauna of atrypids identified as the late Wenlock species *Atrypa harknessi*. These strata have been mapped in the past as Hemse facies, but must correlate with Klinteberg strata: they underlie the Petesvik fauna. The atrypids suggest therefore that these are a southwesterly, distal deeper water facies of the Klinteberg. Locally, large macro-bored domal stromatoporoids and phaceloid rugosans indicate a biostromal facies distal to reefs. Jeppsson and Calner (2001) separated the distal, deeper water limestone facies of this area as the Hunninge Member within the lower Klinteberg Formation, corroborated by atrypid data herein.

On Gotland, the absence of *Spirigerina lockwenia*, and *Ekenia lonsdalei*, species diagnostic of the Much Wenlock Limestone sequence of the British Midlands (*ludensis* Zone), may be due to a lack of appropriate facies outcrops. This species should be present in the high middle to upper part of the Klinteberg succession. Bassett (1974, fig. 2) correlated the lower quarried (Dudley) Limestone at Walsall and Dudley, with the upper *lundgreni* Zone, i.e., below the Much Wenlock Limestone at Wenlock Edge, which lies in the highest *ludensis* Zone. The precise stratigraphic level from which *Spirigerina lockwenia* comes around Dudley is unknown, but this may be the shales within and above the reefal limestones at Walsall and Dudley. This possibility is confirmed in that the *Spirigerina* evolutionary series on Gotland clearly indicates a trend to rib coarsening. Hurst (1975b) stated that *Spirigerina marginalis* in Britain is confined to the *Eoplectodonta duvalii* deep water brachiopod community, but this atrypid is probably *Plectatrypa*, and it seems unlikely that *Spirigerina* on Gotland, a shallower water, peri-reefal inhabitant, would be in deeper water facies in Britain. Moreover, the collecting localities cited are always in the reefal limestones. Hurst (1975b) suggested that "*Atrypa reticularis*", which only occurs in Ludlow rocks on Gotland, is common in the shallow water

Sphaerichynchia wilsoni community of the Wenlock Limestone with more bulbous forms occurring in deeper, quiet water. The species to which Hurst (1975b) refers is probably *Ogylus mildeu*, a deeper water form characteristic of the Coalbrookdale Fm. In the shallower water Much Wenlock Limestone, *Atrypa affinis* appears. The Much Wenlock Limestone contains two species of *Atrypa*, *A. affinis* (Sowerby, 1823), a large, elongate shell, which is present in the lower parts of the Much Wenlock Limestone, and *A. lapworthi* Alexander 1949, a large shell with very flat ventral valve that is more common in the overlying lower Elton beds. In the Midlands, *Endrea lonsdalei* is a part of the Wenlock Limestone sequence, probably mostly collected from the nodular beds or microbial mounds.

The Much Wenlock Limestone in Britain, of late Wenlock age, equivalent in part to the upper Klinteberg limestones, is also generally assumed to be diachronous. The formation, first named by Murchison (1833), is younger to the north-west, so that the shelf margin migrated westwards from the Midlands. Shergold and Bassett (1970), Bassett (1974), Hurst (1975a), and Hurst et al. (1978) suggested that the shales immediately above the Wenlock Limestone, assigned to the Lower Elton beds, might also belong to the *ludensis* Zone at Wenlock Edge. Thus the top of the Much Wenlock Limestone at Wenlock Edge may lie just below the *nilssoni* Zone (Bassett, 1976, 1989; Bassett et al., 1975). Shergold and Bassett (1970) proposed that the more dramatic faunal transition occurs at the boundary between the Lower and Middle Elton beds, rather than the Wenlock Limestone and Lower Elton beds. The facies relationships of the Homeric limestones of the English Midlands and Welsh Borderland are complex, as they represent a carbonate shelf complex with variable, siliciclastic influenced development of nodular wackestones, packstones, silty mudstones, calcarenites, encrinurites, oncoides, microbialites, and patch reefs, from storm wave base through very shallow waters (Ratcliffe and Thomas, 1999). Correlations by Corfield et al. (1992), based on stable isotopic data, clash with those provided by graptolites (Bassett, 1989) and sedimentological evidence (Ratcliffe and Thomas, 1999), so uncertainty exists. The basal Much Wenlock Limestone of the Midlands correlates with the Coalbrookdale Fm. of Wenlock Edge, where reefs are absent at that time, and the Lower Elton beds of the Midlands correlate with the top of the reefal Much Wenlock Limestone at Wenlock Edge (Penn, 1971). Larger coral patch reefs occur in the Wenlock Edge area, at the carbonate shelf edge, and smaller microbial reef mudmounds shelf inwards to the east (Midlands) and south (Malverns). The shelf was approximately 100 km wide and 150 km long, with reefs having been studied by Crossfield and Johnson (1914), Penn (1971), Scoffin (1971, 1972), Abbott (1976), and Riding (1981). The Midlands area, with its microbial and coral mudmounds around Dudley, appears to have produced the greatest brachiopod diversity. Low-relief mounds were 3–5 m thick in the Malverns (Penn, 1971), and 30 m in diameter, and 5 m thick in the Walsall Inlier of the Midlands (Ratcliffe and Thomas, 1999). These had a suggested syndepositional relief of probably less than 1–2 m, providing a suitable base for brachiopod attachment.

The stratigraphic derivation of old atrypid collections is not always clear. Shergold and Bassett (1970), Bassett (1974),

Hurst (1975a), and Ratcliffe and Thomas (1999) do not mention *Spiriferina* in any of their faunal lists for the upper Wenlock limestone succession, and used *Atrypa reticularis* as a catch-all species: their '*Glossia*' refers to *Lissatrypa obovata*. This is probably the result of poor definition of the stratigraphic collecting horizon of most of these old species in museum collections, and the relative rarity of brachiopods in collections. Scoffin (1971, 1972), Penn (1971), and Abbott (1976), who studied the reefs of the top of the Wenlock succession, paid particular attention to the skeletal reef-builders, but treated brachiopods as minor accessories in reef development, and did not discuss the nature of groups such as atrypids. Alexander (1949) described '*Atrypa reticularis*' var. *lonsdalei* (= *Endrea*) from the Wenlock Limestone reefal facies at Dudley; this brachiopod does not occur in the Klinteberg beds of Gotland. Ratcliffe (1988) suggested that the Much Wenlock Limestone of the Midlands was deposited in a shallow mid-shelf setting, using *Girvanella* and *Rothpletzella* oncoids and grainstones as indicators. A similar oncoidal facies locally exists to the NE in the Klinteberg limestones of Gotland, but a study of cements in the grainstones by Frykman (1985) suggests, in contrast, that the Klinteberg oncoids and peri-reefal grainstones were produced in extremely shallow, onshore settings, and were even occasionally subaerially exposed. Mudmounds appear to be lacking in the Klinteberg facies, where stromatoporoids dominate the reef facies.

There is no extinction of any atrypid genera across the Wenlock-Ludlow boundary in northwestern Europe, in contrast with major losses for graptolites reported by Jaeger (1991). Jux and Steuber (1992) identified a positive $\delta^{13}\text{C}$ and negative $\delta^{18}\text{O}$ anomaly for the top of the Klinteberg lowermost Hemse, partly matching the deepening sea-level datum changes. In British sections across the Wenlock-Ludlow boundary there was a 'monotonic decline', but not a sharp anomaly, shifting $\delta^{13}\text{C}$ values from positive to negative values, with a second $\delta^{13}\text{C}$ depletion near the top of the *nassa* Zone (Corfield et al., 1992). Reefs of the lower Klinteberg Formation have produced higher $\delta^{18}\text{O}$ values, which suggested higher salinity to Samtleben et al. (1996). By late Klinteberg time, stable isotopes had dropped to normal background levels of humid periods (Samtleben et al., 2000), or the Klinte 'Secundo episode' of Jeppsson (1990). Jeppsson et al. (1995) discussed the end of the Klinte 'Secundo episode', and the start of the basal Ludlow 'Primo event' of Gotland, and postulated a gap in the matching sections for the upper Klinteberg and lower Ludlow strata of Saaremaa island (Estonia) to the east. In the U.S., Saltzman (2001) recorded a -ve $\delta^{13}\text{C}$ excursion for Oklahoma at the top of the Wenlock, and a +ve $\delta^{13}\text{C}$ excursion at the same level in Nevada, although these may not be so precisely constrained stratigraphically.

In the eastern margins of the Baltic Basin in Lithuania, there is also diachroneity at the Wenlock-Ludlow boundary (Brazauskas and Musteikis, 1991). They suggested, from studying a series of boreholes, that changing atrypid brachiopod communities shifted across the boundary: e.g., *Gotatrypa hedei* (Wenlock in 252 borehole), *Lissatrypa obovata* (Wenlock, rare in Ludlow), *Atrypa reticularis* (Wenlock in the 252 borehole, Ludlow in the 146 borehole), and *Atrypina barrandii* (Wenlock). However, the identification of these

atrypids remains open to revision. They stated that across the Wenlock–Ludlow boundary in this area brachiopod diversity decreased as a result of increased clastic supply from the west, suppressing carbonate sedimentation, and increasing turbidity, and that brachiopod communities shifted across this boundary.

Hemse Formation (Ludlow)

The Hemse beds are roughly 60–140 m thick (Hede, 1960; Jeppsson et al., 1994), and consist of a series of thinly bedded, generally micritic, sometimes biostromal limestones on the NE coast with shaly intervals or partings (perhaps as little as 60 m thick there). Reefal limestones occur in the centre of the island, and shaly, softer weathering deeper water calcareous shales to mudstone units in the SW. Hede (1929) divided the northeastern facies into five vertical stratigraphic units, with the basal unit rich in megalomid bivalves, probably deposited under more restricted conditions. Several of the Hede units contain distinctive, changing atrypid brachiopod horizons. The sequence was divided into three parts by Jeppsson (1983). Hemse reefal facies are less well developed than those of the underlying Klinteberg strata, with more patch reefs and a smaller reef platform. Kershaw (1990), Keeling and Kershaw (1994), and Kershaw and Brunton (1999) have described rocky shorelines, and eroded biostromal tops in the Kuppen and Snabben Hemse sections off the NE coast (Hemse D and E units of Hede, 1929), which suggest that waters must have been periodically extremely shallow, and cyclone or typhoon affected, although not necessarily intertidal there. Samtleben et al. (2000) interpreted the NE Hemse facies as marginal marine and shoal areas. Jeppsson (1987) discussed a 'shale episode' during the *siluricus* conodont Zone, which took place during deposition of the upper Hemse shales: there is no matching anomaly within the atrypid fauna. Bassett (1976) and McKerrow (1979) proposed a transgressive, deepening sea-level event during the *nilssoni* Zone in both Gotland and Britain. This is clearly evident in Britain, but not so marked on Gotland in the shallow water NE facies, except in the presence of more shaly, softer weathering intervals. These shales identify with the appearance of the genus *Atrypa*, which provided several species in succession. Most genera from the Wenlock strata persisted into the Ludlow, but *Atrypa* appeared here for the first time. *Lissatrypa*, from the Elton beds of England, associated with deeper waters, never appeared in Gotland.

In the NE coastal sections, the atrypid communities begin with a rich *Atrypa sulcata* assemblage near the base of the Hemse beds (units A–B, ca. 12 m thick: *nilssoni* Zone, lower Gorstian). This atrypid species occurs with abundant smooth athyridids (typically *Didymothyris didyma*), and is most common between the heads of bulbous stromatoporoids (see also Kershaw 1981, 1990, for stromatopore ecology). Not uncommonly there are nests of *Atrypa sulcata* lodged in between the knobs and crevices of stromatoporoids such as *Densastroma*, suggesting that some of them may have had a pedicle attached to either live or dead sponge heads. Along with *A. sulcata* there are rare specimens of *Atrypa* cf. *reticularis*; however, the latter species is more typical of the higher Hemse 'C' units (lower *scanicus*

Zone). The *Atrypa* and *Atrypa* assemblages appear to have lived apart, with *Atrypa* replacing *Atrypa sulcata* from the lower Hemse succession, as they almost never co-occur. Interbeds of other brachiopods in these lower units include abundant *Protochonetes* and *Didymothyris*, without atrypids and stromatoporoids. Higher in the NE facies (Hemse C: upper *scanicus* Zone), *Atrypa prunum*, a globose species nearly twice the size of ancestral *A. sulcata*, became abundant, also commonly with abundant bulbous stromatoporoids, and also shell-bed forming. Some of the loose and broken *Atrypa* shells show reworking, and overgrowth by calcareous algae or tabulate corals and bryozoans, which points to slow rates of sedimentation, some transport, and reworking of the substrate. *Atrypa reticularis* disappears at this level, to be replaced by a smaller, narrower species with wider frills, *Atrypa sowerbyi* Alexander (1949) which persists into the highest units (D–E) of the Hemse beds in the NE within the *tumescens*–*leintwardinensis* zones.

In the central, reefal facies of the Hemse beds (upper Gorstian, *tumescens* Zone), *Spirigerina marginalis*, from the Klinteberg succession, is replaced by *S. costata*. *Atrypa prunum* is replaced by *A. hemsea*, although stratigraphically also slightly higher than *Spirigerina costata*, which tends to occur in the lower reefal facies. Reefs appear to be common in the middle to upper Hemse beds, and even range into the Eke Fm. Watkins (1975) documented the presence of '*Lissatrypa sulcata*' [= *Atrypa hemsea*] in dense, rich nests or pockets in reefal settings of the Hemse strata on the central south coast around Ljugarn (see also Samtleben et al., 2000, pl. 4, fig. 5, for *Atrypa hemsea*). In the higher, upper Gorstian *tumescens* Zone, *Atrypa reticularis* is replaced by common *Atrypa sowerbyi* in biostromal and shallow marginal marine areas.

To the SW, in the soft-weathering, shaly, deeper water settings of the Hemse strata, a different atrypid fauna occurs in the Petesvik Bay area. Munthe (1911, p. 1400) termed this the 'Petesvik (Hablingbo) fauna', and correlated it with the Östergarn fauna, which is now believed to be somewhat younger. The Petesvik locality appears to have the youngest *nilssoni* fauna known on Gotland. Here the abundant atrypid present is *Atrypa purchisoni* Alexander (1949), a small species with its British counterpart in the lower Elton beds of Shropshire. It occurs in deeper water facies on Gotland together with common small *Cyrtia*, *Leptaena*, and other strophomenids, very small solitary rugosans, and small hemispherical favositids and heliolitids (diameter <5 cm). Stratigraphically *Atrypa purchisoni* (units A–B) precedes the much larger species *Atrypa reticularis* of the NE coast (unit C), and the latter may be its descendant. At Petesvik there is also *Septatrypa petesvika*, a small, narrow, relatively flat smooth species that has not been found either in England, or in the NE facies of Gotland. The deeper water facies of the SW continues into the middle and higher Hemse beds with the deeper water *Davia* (athyridid) brachiopod community in which are rare clusters or nests of *Atrypa sowerbyi*. *Davia* itself is commonly nested in clusters on the soft substrates, with the umbo down (personal observation).

On Gotland, the middle to upper Hemse beds (ca. 31 m thick?), within the *Atrypa reticularis*, *A. sowerbyi*, and *Atrypa prunum* – *A. hemsea* zones, episodic erosional inter-

vals, marked by rocky shorelines, have been documented by Keeling and Kershaw (1994). Whether these represent emergence of the shoreline carbonates, and the removal of significant sediment, is unclear. Broken, eroded, and interrupted growth of the onshore shallow carbonate platform benthic community, in water depths of <5 m is a common event in the equatorial, monsoonal storm belt today. Tropical typhoons or hurricanes represent mass destruction events in which the entire local community, and substrate, can be destroyed and removed: such events could easily be mistaken for emergence. At any rate, *Atrypa* and *Atrypoides* thrived here, and broken shell beds of these taxa are common. The atrypid communities were able to re-establish themselves repeatedly after storms during deposition of the entire Hemse sequence. This pattern of growth and recuperation was also followed by accompanying stromatoporoid clusters and thickets, as shown by Kershaw (1990). *Atrypoides* commonly lived in between such domed stromatoporoids (with small shells observed directly as nestled in between domes and branching portions of the coenostea), although liberosessile, convexo-plane *Atrypa*, losing their pedicle in adult stages, generally favoured soft, level bottom substrates for the use of its frills. Some *Atrypa* shells were commonly broken, with frills shattered, and reworked in some levels.

In Britain, the Elton beds (*nilssoni*–*scanicus* zones) consist of soft-weathering calcareous shales and thinly bedded limestones that cap the Much Wenlock Limestones: they are time equivalents of the lower Hemse strata in Gotland. The Lower Elton beds contain a very rich, but low-diversity atrypid fauna, especially well developed around Wenlock Edge in the Shadwell Quarry, where the contact with the underlying Wenlock Limestone is exposed. Lawson (1960) cited '*Atrypa reticularis*' and '*Glassia*' from the lower Elton beds. *Lissatrypa obovata* occurs in the Much Wenlock Limestone below, and *A. reticularis* sensu stricto in the higher Bringewood beds above. In the lowest 5 m of the Elton beds, the large shelled species *Atrypa lapworthi* Alexander (1949) occurs, followed 5–7 m above the Wenlock Limestone contact by the smaller sized shell of *Atrypa munchisoni* Alexander 1949. The latter species is present in the lower part of the Hemse beds (*nilssoni* Zone) in the SW facies on Gotland. *Atrypa reticularis* s.s. is a shallower water species, and probably does not occur in the deeper water upper Elton beds of Britain, equivalent to the *scanicus* level in the Hemse beds. Smooth shelled *Lissatrypa obovata* (Sowerby, 1839) has been listed from the lower and middle Elton beds by both Lawson (1960, 1975) and Watkins (1979), with the latter defining a '*Glassia obovata* Association' for this level. I have examined the Watkins collection of '*Glassia*' and confirm that it is a small species of *Lissatrypa*, of a size similar to Llandovery *Lissatrypa*. This should thereby be renamed the '*Lissatrypa* Assemblage' in Britain. At the Shadwell quarry *Lissatrypa* seems to be absent, but Watkins (1979, p. 208) stated that this species increased in abundance in the middle Elton beds mudstone facies. Musteikis and Juskute (1999) and Musteikis and Paskevicius (1999) identified a widespread, deep water '*Glassia obovata*' community from borehole samples in Lithuania on the eastern margins of the Baltic Basin. This matches the *Lissatrypa* community of Watkins (1979) from the lower Ludlow (lower Gorstian) Elton beds of Britain.

The succeeding Bringewood beds of Britain fall primarily within the *tumescens* Zone [i.e., somewhere within the middle to upper Hemse strata]. Their brachiopod fauna has been studied by Watkins (1979), and Watkins and Aithie (1980), who concluded that there was an '*Atrypa reticularis* – coral association' in the upper Bringewood beds, 'Aymestry Limestone' facies, with abundance of up to 20 shells per square metre. Watkins (1979, p. 225) illustrated loose valves of unidentifiable *Atrypa* from the *Mesopholidostrophia strophomenid* association of the Bringewood beds. *Atrypa* '*reticularis*' (Linnaeus, 1758), sensu lato, appears to occur in England in the lower part of the Aymestry Limestone, a carbonate facies allocated to the upper Bringewood beds by Lawson (1960, p. 118; 1975), who mentioned that *Monograptus leintwardinensis* occurs in the Aymestry Limestone. Cherns (1988) stated, 'the basal beds of the Lower Leintwardine Formation . . . are developed as carbonates within the top part of the Aymestry Limestone', thus correlating the Aymestry Limestone as a reefal facies of the Leintwardine Formation. She further remarked on the top of the Aymestry Limestone at Aymestry corresponding to an 'erosional planed surface', filled in part by Bringewood fossils, i.e., suggesting a local disconformity here. Cherns (1988) stated that around Ludlow, the brachiopods '*Atrypa reticularis*' and *Isorthis orbicularis* were the dominant elements of the Lower Leintwardine sections, and that *A. reticularis* was also the dominant component of the upper Bringewood fauna (*tumescens* Zone) underneath. This '*reticularis*' may refer to *Atrypa sowerbyi* Alexander (1949). Alexander's (1949) species *Atrypa sowerbyi* is said to have been collected from the older Dudley Limestone of the Dudley area, whereas *Atrypa sedgwicki* (= *Atrypa reticularis* s.s.) came from the 'Aymestry Limestone' of the Craven Arms area of Shropshire. This suggests that the 'Aymestry Limestone' of these two localities are of different ages, with the Dudley 'Aymestry Limestone' representing the younger level within the *tumescens*–*leintwardinensis* zones, and the Craven Arms 'Aymestry Limestone' being of *scanicus* age.

Eke Formation

The ca. 10–15 m thin Eke Formation (Ludfordian, probably *leintwardinensis*–*bohemicus* zones) is dominated by a crinoidal to reefal facies in the NE of Gotland, which gave way to restricted shallow lagoonal, or proximal shelf, calcimicrobial, oncolitic facies in the southwest. This marks the disappearance of deeper water, western, distal brachiopod shelf facies on Gotland. Cherns (1982, 1983), in her extensive sedimentological study of the Hemse–Eke transition and Eke lithology, concluded that tidal erosion surfaces, desiccation structures, stromatolites, and paleokarst features indicate temporary subaerial exposure of parts of the formation, and generally very shallow water, including intertidal conditions. However, the atrypids appear to be excluded from the shallowest, intertidal to subaerial developmental stages of the Eke strata. Two taxa occur: *Endrea ekenia*, present in locally great abundance in the crinoidal NE facies around Lau (in old collections these occur by the drawer full), and *Atrypa alata* which can be shell-bed forming in the oncoidal *Rothpletzella gothlandicum*, calcimicrobial facies to the SW (Rothpletz, 1913). *Atrypa alata* is commonly almost completely

covered by oncoids of the cyanobacterium *Rothpletzella*, yet with commissures free, and shells capable of opening, a peculiar association which suggests that these frilly shells could survive in very shallow subtidal waters of possibly less than 1–2 m depth. Here shells were constantly overturned, and high salinities, or stagnation, may have been common. This would corroborate the arid period interpretation of Samtleben et al. (2000) for the Eke beds. These shells are indicated as *Atrypa reticularis* by Stel and de Coö (1977) and as *Atrypa* sp. by Cherns (1983, p. 22). *Atrypa sowerbyi* is absent in either facies, and appears to have disappeared in the Gotland area prior to the deposition of the Eke beds. In the Eke beds and higher on Gotland, there are also no shells of *Atrypa*.

In Britain the Eke strata equivalents are generally considered to be the middle to upper Leintwardine Fm., and higher silty to sandy siliciclastic Whiteliffian strata. *Atrypa reticularis* sensu lato is reported in England from these higher levels of the Leintwardine Fm. (Lawson, 1960), but *reticularis* sensu stricto is absent in the Eke beds, being replaced by *Endrea ekenia* in the biostromal facies, and *Atrypa alata* in the oncolitic facies. In Britain, Alexander (1949) described *Atrypa woodwardi* from the *Dayia navicula* beds [lower Ludfordian?] at Dinchope, Shropshire, which is somewhat similar to *Atrypa alata*, but is smaller, and lacks the well-developed frills of the Gotland species. The Ludfordian in Britain is primarily a siliciclastic facies with an impoverished brachiopod fauna in which atrypids are scarce or absent.

Burgsvik Formation

Overlying the Eke beds are the Burgsvik sandstones, variably up to 47 m thick, with the upper 2 m consisting of oolites and pisolites interbedded with sandstones (Stel and deCoö, 1977; Sundquist, 1982a, b); these authors mention small *Atrypa* in the Burgsvik sandstones. These are of middle Ludfordian (early Whiteliffian, probably *bohemicus-kozlowskii*) age. The sandstones thin out to the NE to less than 8 m, being partly reefal and oolitic shoals there. Very few whole shells occur in the Burgsvik sands: most are disarticulated, worn and poorly identifiable *Atrypa* cf. *woodwardi*.

Hamra/Sundre formations

The Hamra beds, of upper Ludfordian age (*formosus* Zone) vary from 20 to 40 m in thickness, and have been divided by Jeppsson (1983) into three units, a lower nodular algal-microbial unit, and higher reefal and inter-reefal limestones and shales. These upper Ludlow strata are said to mark the arrival of a Secundo (dry) state of Jeppsson (1990), and an H (humid) period of Samtleben et al. (2000), so that the two models appear to clash here. The reefal limestones locally contain rich, in situ pockets of the reef-dweller *Spirigerina quinquecostata* (Munthe, 1911; Hede, 1960, p. 65), but other atrypids are scarce. Rare specimens of *Reticulatrypa* (first appearance on Gotland), *Atrypina*, and *Atrypa* occur elsewhere in peri-reefal sediments. The shallow water nature of both stratigraphic units excluded the deeper water atrypid taxa, and the atrypid record of Gotland tapers off in these upper units in both diversity and abundance, coinciding in general with most areas elsewhere except in the Urals and Central Asia. In Estonia, the age-equivalent of the Hamra/

Sundre, i.e., the Kuressaare beds, carry an *Atrypa* *saaremaensis* fauna (Copper, 1977a).

The Sundre beds are the uppermost strata exposed in the southern parts of Gotland: the lithology consists of ca. 10 m of reefal and inter-reefal limestones with rare brachiopods (Kano, 1989). Reefs are atoll-like and very shallow water faro (small pinnacle) structures with central lagoons (Samtleben et al., 2000). In the Sundre reefs on the south coast occurs *Reticulatrypa*; other atrypids are scarce, possibly explained by the repeated emergence of the faroes and the very shallow water settings prone to storms or restricted water conditions. *Reticulatrypa* is normally a Lochkovian–Pragian genus, suggesting that the Gotland species is early, pre-dating other Pridoli occurrences. Nevertheless, the Gotland and British marine sections end with at least a late Ludlovian fauna, basically confirming the concept of Bassett et al. (1989, fig. 126) that the youngest outcropping strata on Gotland may have been above sea level in the Pridoli and that marine Pridoli age ‘Beyrichien Kalke’ occurred in deeper waters to the south of the island. There is no firm evidence for the presence of Pridoli genera such as the Uralian and central Asian atrypids *Atrypinella*, *Zeravshania*, and *Istokina*, although *Reticulatrypa*, a close relative of these two, is already present. There is also no evidence for the appearance of taxa known from the Urals such as the Ludlow genus *Procarinatina* Mizens and Sapelnikov 1982 [see Sapelnikov, 1964], Ludlow–Pridoli *Crassatrypa* Mizens 1977 (the ancestor of the Karpinskiinae), the Pridoli–Emsian genus *Plesicarinatina* Mizens 1977 (ancestor of the Carinatininae), the unusual divaricate Ludlow–Pridoli genus *Symmatrypa*, nor the common Ural forms such as *Gracianella* (*Gracianella*) and *Gracianella* (*Sublepada*). The Urals and Central Asia were a region of brachiopod innovation in the Ludlow–Pridoli (Sapelnikov et al., 1987; Sapelnikov and Mizens, 1991), but this evolutionary development is apparently missing in northwestern Europe. A possible reason for this might be that this belt was probably a part of the north-eastern shelf of Baltica (or the Siberia plate), north of the equator, and thus currents would have swept larvae N of Baltica over to North America, where *Gracianella* is present. There is a single record of *Gracianella* (*Sublepada*) from boreholes in Lithuania, which needs to be confirmed, as these have neither been illustrated nor described (Brazauskas and Musteikis, 1991). Western Siberian faunas also have similarities with those of the Baltic Plate, e.g., as seen in the presence of taxa such as *Atrypa* (Kulkov, 1990).

Five described glacial erratic species of uncertain stratigraphic age, probably derived from Gotland or the seafloor south of Gotland, were not investigated, as the type collections were not available. These include, in the order described, *Glasia laevigata* (Kunth, 1865), *Reticulatrypa micula* (Richter, 1866), *Septatrypa succissa* (Richter, 1866), *Atrypina gallina* (Haupt, 1878), and *Septatrypa trilobula* (Roemer, 1885). A number of these may have been of Pridoli age, as seen from ostracodes dredged from deeper waters off Gotland (Martinson, 1967).

Form and function in Atrypida: external

The shell of most Silurian atrypids conforms to a relatively simple pattern: it is relatively round to ovate, more or less

biconvex (but varying from ventribiconvex to convexo-plane), and smooth or ribbed (sometimes with frills, but spines were never well developed). Most had a functional pedicle muscle, although some of these lost the pedicle muscle during ontogeny, and switched to a liberosessile mode of life as adults. The shell wall was impunctate, consisting of a very thin, granular, primary layer, and thicker, secondary layer of obliquely, roughly radially directed prismatic crystals. They had a ball (tooth) and socket, shell opening-closing mechanism of the cyrtomatodont type, and an astrophic hinge. Strophic hinges, ventral valve cementation, fenestration of the shell wall, and extensive spinosity were only developed in specialized side-lines of atrypids later in the Early Devonian and in the Anazygidinae (see *Zygatrypa* herein). Internally, the dorsal valve was typified by medially directed (Glassiinae), mediodorsally directed (Anazyginae), or dorsally to dorsomedially directed spiralia (the rest). Only one primitive group, the Anazyginae, 'living fossils' in the Silurian as most were extinct by the end Ordovician, possessed a jugum; others had separated jugal processes tipped by various types of specialized jugal plates. [The 58 main character states used to classify the atrypids are cited in Table 1.]

The shell wall was examined by scanning electron microscopy for nearly all species. The outer, primary layer is very thin, normally less than 10 microns, and thus easily eroded. Its structure is granular, consisting of relatively irregular, short, variably formed crystals (Fig. 4). Underneath the primary layer is a much thicker secondary layer composed of long, straight, flattened, tightly bundled crystals, about 10× wider than thick. The primary layer may incorporate ornamentation at a fine scale, e.g., fine concentric ridges or filae (as seen in *Spirigerina*), and also fine radial striations and ridges, which are sometimes in zigzag format (e.g., in *Xanthea*). In the atrypids with ribs, these fibrous crystals are radially aligned, parallel to the ribs. In smooth atrypids, however, there is considerable variation in the shape of these crystals: many are curved, and mostly they are irregularly overlapped to form a kind of cross-hatched network, as seen in *Lissatrypa* and *Atrypoides*. This difference appears attributable to additional strength required for the shell wall of smooth atrypids, derived from this random overlapping.

Ribs

Atrypids may essentially be divided into smooth or ribbed forms. In some groups, there was an evolutionary trend to secondary smoothing of the ribs during ontogeny, and in one species, *Atrypa* (*Atrypa*) *gotha* n. sp. from the Upper Visby Formation of Gotland, the growth lamellae converted to nearly smooth fringes. Ribbed forms increased shell strength by corrugation of the shell. With the abundance of well-preserved shells available, an attempt was made to devise a system to denote branching and intercalation of surface ribs, as for *Atrypa sowerbyi* from the upper Hemse beds by Harper (1969). This system was abandoned, as no specific rib multiplication patterns could be determined in the Atrypinae. Even for the Spirigerininae and Plectatrypinae in which double or multiple rib-pairs form a ventral carina along the plane of symmetry, no consistent or uniform trends in rib branching or intercalation could be found. In the evolution of the atrypids, growth interruptions in the advancement of

the shell margin evolved into a trend where the shell periodically retracted the mantle, and started to produce a new layer underneath the last shell margin. This renewed growth resulted in overlapping of the shell margin, the production of short growth lamellae initially, and later the evolution of frills (or spines) which enabled the shell to expand its margins well beyond the available body cavity. The first short frills are seen in *Gotatrypa* and *Oglupes* during the latest Telychian, and in *Atrypa* in the early Homerian of the Baltic Basin (Fig. 5). This feature may have appeared earlier elsewhere, but no extensive frills have yet been found, just short growth lamellae. Although initially frills may have been an asset to stabilize the shell, to conquer substrate territory, to avoid predation or parasites, or even to filter out coarse sedimentary particles, frills may later have ended up as a liability. During the Ludlow, *Atrypa* also discovered a way to solve this problem of cumbersome frills. To shed its frills, some developed an ingenious trick: perforations along the fringe, where the frill raised itself away from the shell surface acted as a means of detaching the frill, at least on the dorsal valve, which lay uppermost. This meant that only the last frill was maintained on the dorsal valve; others were systematically shed during growth (Fig. 4), a possible advantage in higher energy, shallow-water or storm-disturbed settings.

Ribs and growth lamellae gave the shells of many atrypids the possibility to develop an array of structures. One of the first of these was to extend the growth lamellae as sharp points, along the base of the rib troughs, i.e., a kind of short spine as seen in many *Gotatrypa* in the Llandovery and later. The evolution of spines along rib crests during the Wenlock is another example. Spine development became possible when a side branch in the subfamily Plectatrypinae evolved coarse ribs and extended rib crests that grew faster than the adjacent rib troughs. With curling of this extended rib crest, short and blunt spines, or simply rib caps (capidulae), were produced. The latter feature evolved partially in a finely ribbed version of *Plectatrypa*, the late Wenlock subgenus *Gutnia*. The earliest known spinose atrypid on Gotland is *Eospinatrypa hallae*, from the Halla Formation, which has the same zigzag micro-ornament as *Xanthea*, but has lost its carination and evolved short, irregular spines. It is sometimes difficult to distinguish between advanced *Xanthea*, such as *X. haruspex*, and early *Eospinatrypa* shells, underlining their linkage and ancestry. The development of spines simply resulted from the infolding of the projecting rib crest extension, and curling to produce a hollow tube. The spines are thus always hollow, as seen in serial sectioning (Fig. 6).

A correlation between ribbed and smooth shells and their distribution within benthic communities was not apparent. Smooth *Atrypoides* adapted to shallow water settings on Gotland, while smooth *Lissatrypa* in Britain occur in a broad range of settings, commonly from deeper muddy bottoms and rarely from shallow peri-reefal settings. Smooth *Glassia* were exclusively deeper mud bottom inhabitants. The oldest *Lissatrypa* species, from the Aeronian of Anticosti Island, were deep-water dwellers in the *Clorinda*-graptolite community of BA-5 (Copper, 1973a), but by the Telychian had moved to shallower regimes as well. The smooth genus *Septatrypa* generally occupied biostromal settings on Gotland (it was absent in Britain), but could also occur in the deeper

Fig. 4. Shell wall structure of atrypids via SEM. (a) Rhythmic overlap of primary and secondary layers in *Oglupes muldea* n. sp., $\times 1140$; (b) secondary layer crystals in *Spirigerina quinquecostata*, $\times 624$; (c) irregularly, cross-hatched, overlapping secondary crystals in *Lissatrypa obovata*, $\times 126$; (d) growth interruptions in smooth, primary shell wall of *L. obovata*, $\times 82$; (e) concentric-radial surface sculpture in primary layer of *Spirigerina quinquecostata*, $\times 54$; (f) zigzag micro-ornament of *Xanthea scabiosa*, $\times 52$.

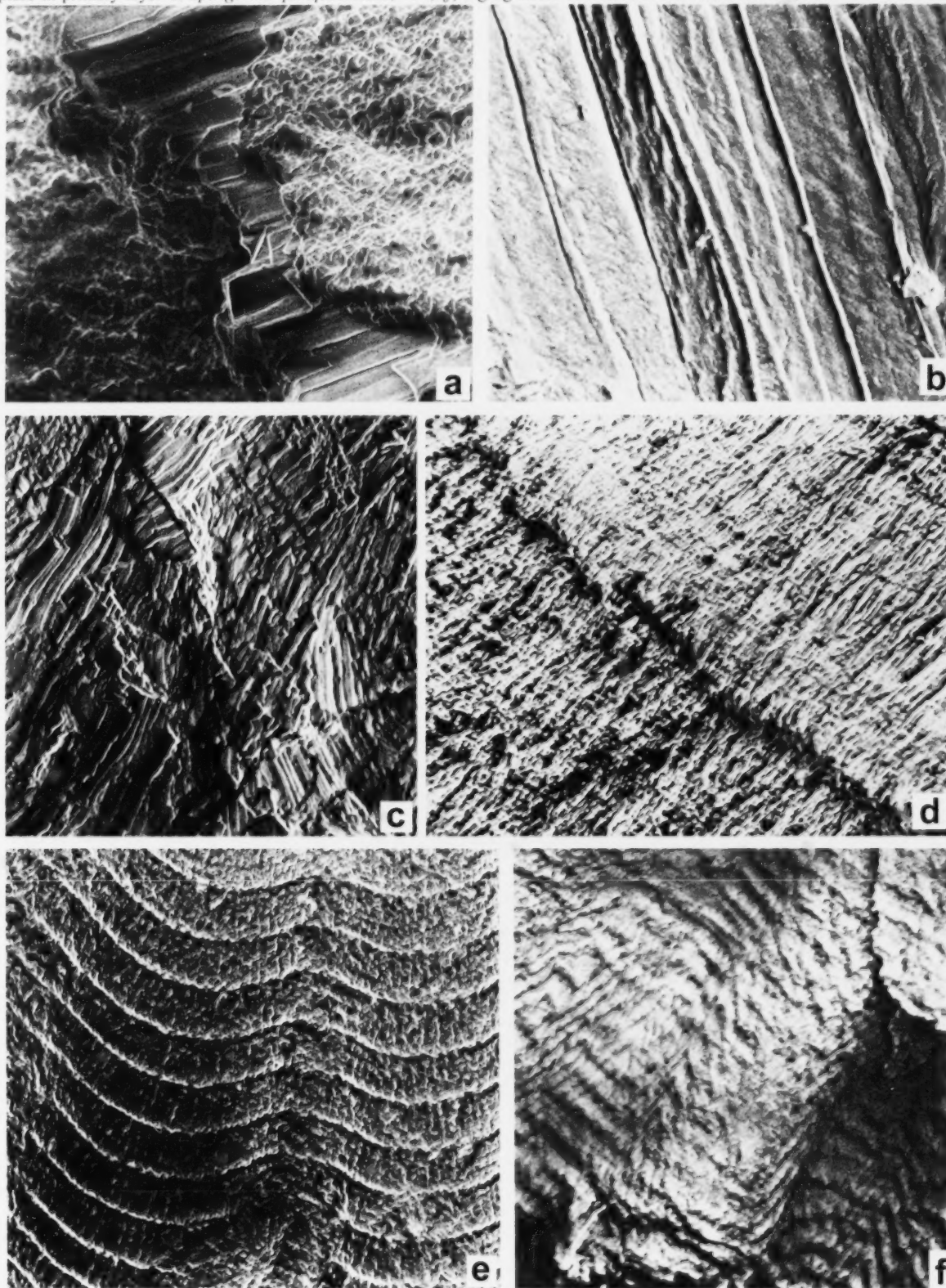


Fig. 5. Ribs, frills, and growth lamellae via SEM. (a) Postage stamp-like, elongate rib perforations of *Atrypa* (*Atrypa*) *sowerbyi*, through which an underlying growth lamella is visible (perforation in black), $\times 46$; (b) dorsal side frill of same shell, *A. (A.) sowerbyi* with fine perforations, $\times 5$; (c) ragged, irregular short growth lamellae of *Gotatrypa hedet*, $\times 18$; (d) relatively flat ribs, growth lamellae of *Oglupes visbyensis*, $\times 27$; (e) concentric ridges of *Atrypina barrandii* (these shells have no growth lamellae), $\times 43$; (f) short growth projections in the rib troughs of *Reticulatrype hamrae*, $\times 118$.

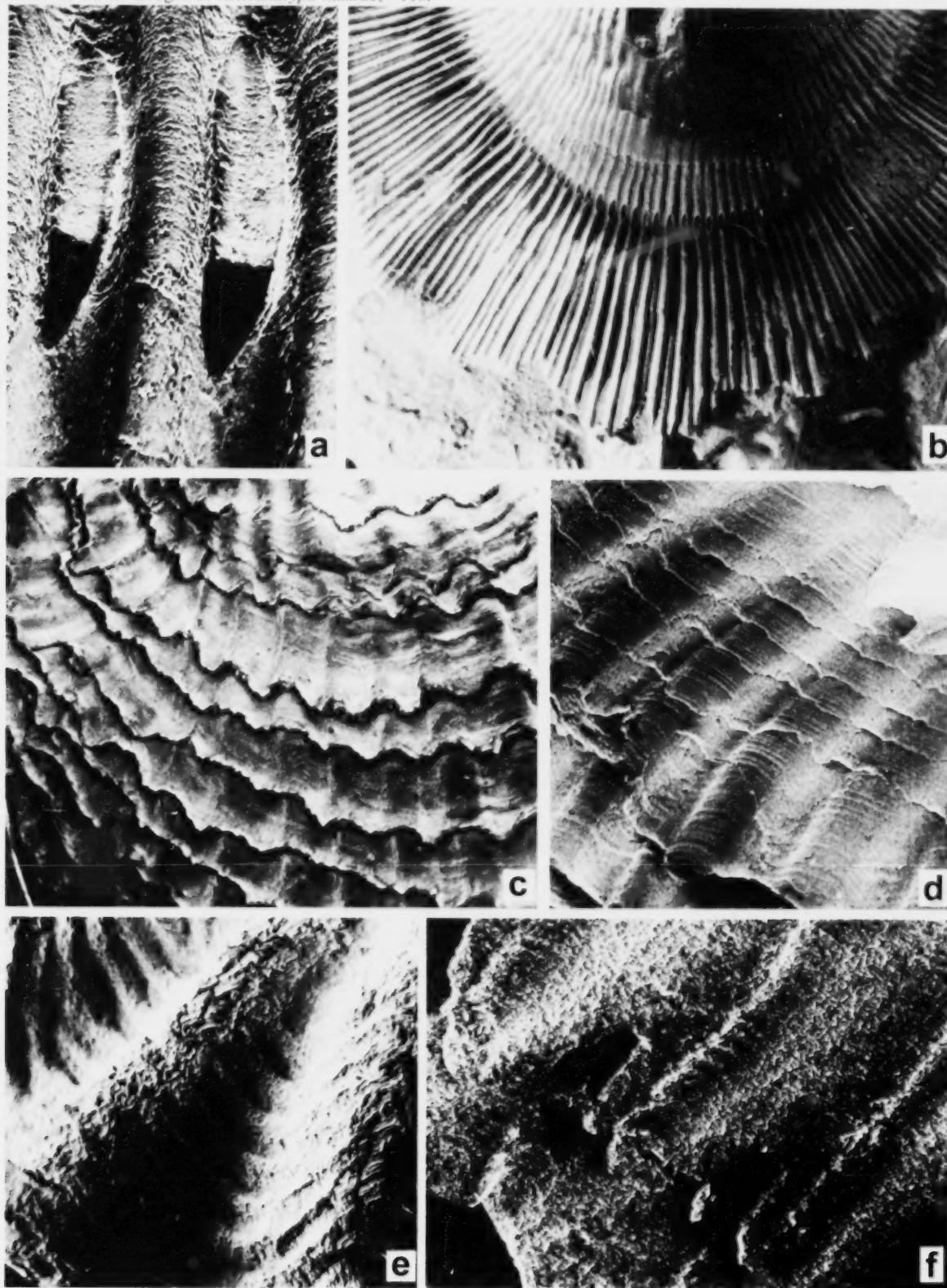
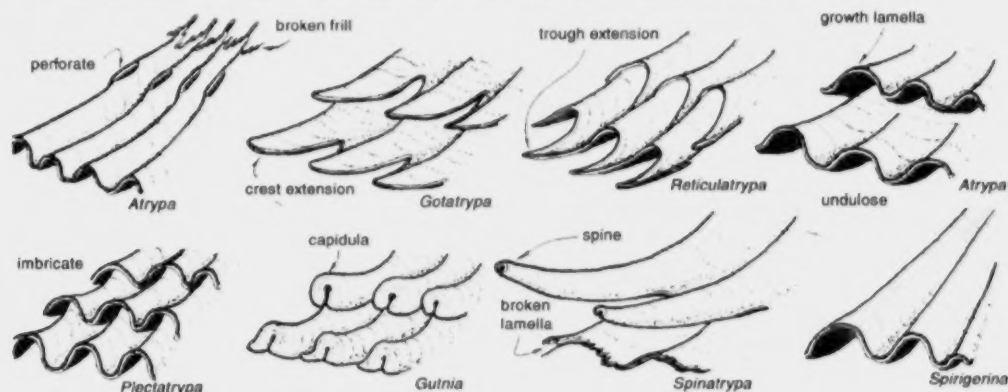


Fig. 6. Surface ornament in Silurian ribbed atrypids. Ribs and growth lamellae produced a series of permutations which gave atrypids the opportunity to strengthen the shell, to deter parasitic epibionts, to improve filter feeding (channeling currents, sieving strains), to protect the anterior commissure from predators (overlapping growth lamellae), or to provide stability on unstable substrates (e.g., frills, spines). Considerable flexibility of form existed in the surface ornament of *Atrypa*, e.g., the evolution of perforations to shed frills, and undulose, or wave-like growth interruption between the start of each growth lamella. Figures not to same scale.



water *Atrypa murchisoni* community of the western Hemse facies. In the Llandovery of Anticosti Island, *Septatrypa* initially was most abundant in reefs and peri-reefal strata (Aeronian), but later also in the mid-shelf *Stricklandia* community (Telychian). The same reefal niche was observed by Jones and Hurst (1984) for the genus *Septatrypa* (= *Dubaria*) from the Llandovery of Greenland. Thus, *Septatrypa* shifted from shallow to deeper waters in the Early Silurian. Ribbed atrypids were also spread across a broad spectrum of water depths and substrates: within genera, rib density did not change with the shelf transect from onshore to offshore. Finely ribbed and coarsely ribbed forms were found in all habitats. Carinate shells, those shells with a keel on the ventral valve (produced by a pair of enlarged ribs in the plane of symmetry), and corresponding groove on the dorsal valve, include the genera *Spirigerina*, *Atrypina*, *Plectatrypa*, and *Xanthea*. *Spirigerina* was almost exclusively a pedicle-attached, peri-reefal and reef inhabitant: a keel may have functioned as a streamlining device in this genus, but the significance of this is not obvious. Keeled shells like *Atrypina* favoured both deeper settings (Buildwas Formation in Britain), but also the shallow setting of the Much Wenlock reefs. Keeled *Plectatrypa* spanned communities in mid-shelf to shelf edge settings. The carinate genus *Xanthea* was also a reef inhabitant. Thus keels or carinate shells were more common in higher energy habitats, but their ancestors in the late Ordovician, *Eospirigerina*, occupied both deeper and shallow water settings.

Sizes of shells

The Silurian atrypids of NW Europe had a relatively wide range in size and shape, from small taxa in which adult shells failed to reach a width of more than 5 mm to those in which frills added space to shells more than 35 mm wide, from globose to relatively low forms, from forms with a narrow hinge to those which had a wide hinge, from shells possessing a high anterior fold to those which were rectimarginate or sulcate, and from those with a pedicle foramen

to those that lost one. The significance of size and shape is not always readily evident, and general trends cannot always be plotted to extract a meaning. Small size appears to be favoured, or to be the limitation in deeper water habitats for some genera. *Zygatrypa*, *Lissatrypa*, *Glassia*, and *Atrypina* maintained a relatively small size (<5–10 mm width): all of these are common to abundant primarily in the deeper water, offshore community (BA-5), and rare in the shallowest water communities. The exception to this may be *Atrypina*, which also occurs in reefal, higher energy environments in the Hamra-Sundre beds. Sampling may also produce a bias against the smaller taxa, since such shells are easily missed, unless samples are collected in bulk and sieved. Large sizes, such as shells with frills, occur in both deeper (e.g., *Oglupex visbyensis* in the Lower Visby beds) and shallower water settings (*Atrypa alata* in the oncoid shoal habitat of the Eke beds). In a study of British '*Atrypa reticularis*', Fürsich and Hurst (1974) were able to state confidently that 'spiriferides . . . do not decrease in size towards deeper water, the result of their highly efficient lophophore'. This is generally contradicted by the Gotland and British atrypid data. They complemented this with the observation that 'brachiopods living in deeper water may be at a disadvantage in collecting food, as there is less available'. The correlation between water depth and food supply is tenuous: deep waters may be as rich, or richer, in nutrients as shallow waters, a factor dependent on upwelling, surface plankton production rates, particulate organic matter (POM) or dissolved organic matter (DOM) recycling in the water column, bacterial abundance, and rate of nutrient supply to the deep sea (i.e., consumption of food on the way down). Although larger atrypid species of the same genus generally have more spirallial whorls, since increasing volume can accommodate a larger lophophore, there was no direct correlation observed between water depth, shell size, and spirallial size. Some taxa belong to families in which smaller size appears to have been advantageous, e.g., the Anazyginae, Atrypinae, Plectatrypinae, and Spirigerinae. None of these genera reached very large size.

Convexity

Convexity can be variably interpreted: in general no recognizable deep versus shallow water patterns were observed. Fürsich and Hurst (1974), studying Silurian brachiopod communities of England, suggested a correlation between flat shells and soft bottoms, and biconvex shells with turbulence. Hurst (1975c), who studied Gotland brachiopod ecology, suggested that *Atrypa* was more 'bulbous' (more convex?) in deeper than shallower waters, but it is not known what taxa he included in this database, and from where. This correlation was not directly apparent in shells studied here. Strongly biconvex *Glossia*, *Gotatrypa* (e.g., *G. hedei*), *Oglupes davidsoni*, and *Plectatrypa* usually occurred in deeper water communities on Gotland, but in shallow waters highly biconvex to dorsibiconvex forms also were common, e.g., *Atrypoides*, *Eospinatrypa*, and *Plectatrypa* (*Gutnia*). Flat-shelled, convexoplane *Atrypa* occurred in both deeper water settings, e.g., *Atrypa purchisoni* (SW facies of the Hemse beds, Gotland, and lower Elton beds in Britain), and in shallow oncoid shoals, e.g., *Atrypa alata* (Eke beds). Wider, longer-hinged shells of *Xanthea* appear to be most common in the patch reef to reef complex settings of the Upper Visby through Slite beds: this is difficult to compare as such longer-hinged forms are not otherwise known in the Silurian.

The development of a prominent fold on the anterior commissure was related to filter feeding. With inhalant currents being pumped in by the lophophore from the sides, as in modern rhynchonellids, it would have paid shells to utilize an effective exhalant waste pipe, the anterior fold. It is difficult to visualize any other morphologically efficient filter-feeding system, e.g., one in which the intake food supply would be restricted to a narrow canal at the anterior, and the exhalant wastes being broadcast in a wide path on all sides. Contamination of intake with waste would be inevitable. Effective waste elimination, the 'sewage pipe' strategy, could be provided by a strong, U-shaped fold, as seen in many atrypids. Fürsich and Hurst (1974) postulated that a strong anterior fold would benefit brachiopods in quiet water settings. This makes sense, as waste elimination is not a problem for any shallow water, turbulent reef and carbonate biota. But did a correlation exist between energy and fold size in the Silurian atrypid community? The narrowest anterior folds were exhibited by *Plectatrypa*, *Xanthea*, and *Gutnia*. *Plectatrypa* was generally a deeper water inhabitant (ca. BA-4), but it also occurred in the deeper patch reef setting of the Upper Visby beds (*Plectatrypa abbreviata*), and the biostromal setting of the upper Slite (*P. parimbricata*). *Gutnia* and *Xanthea* were shallow reef inhabitants (BA-2-3), with the earliest occurrences of *Xanthea* also noted in the deeper patch reef setting of the Upper Visby beds. *Plectatrypa* were not normally found in the shallowest settings, or in the deepest. Within both *Gotatrypa* and *Atrypa* there was considerable species-to-species variation in the height of the anterior fold, but no direct association between shallower and deeper inhabitants. In the smooth, shallow, sheltered water species *Atrypoides prunum* (Hemse beds), gerontic shells had a marked U-shaped anterior fold, but the average adult shell had only a gentle fold: here a fold was a factor of old age, with neanic specimens up to 20 mm wide being roughly rectimarginate.

Pedicle structures

Some atrypids showed variable development in the curvature of the area, beak, and disposition of the foramen, the opening for the pedicle muscle. In others, the foramen was a fixed, invariable feature. In the fixosessile reefal genera *Spirigerina* and *Xanthea*, deeper to shallower water genus *Atrypina*, and generally deeper water genus *Plectatrypa*, the orientation of the area was almost always simply orthocline, with an apical foramen surrounded by two prominent deltidial plates. This meant a shell attached by a pedicle muscle at all stages in life. Fürsich and Hurst (1974) suggested such a shell feature was typical of more turbulent conditions, where a holdfast was essential. However, *Atrypa reticularis* from the shallow water NE Hemse facies, where water energy would be expected to be higher, lacked a pedicle opening, and was no different from its deeper water Hemse form *Atrypa purchisoni* in the SW facies. It was not until the Devonian that atrypids developed techniques to cement the ventral valve to hard substrates, thus, this option was not available to Silurian forms. The smooth taxa *Septatrypa* and *Glossia*, both generally deeper water inhabitants (respectively, communities BA-4 and BA-5), also show pedicle attachment throughout life, an apical foramen and small deltidial plates, although the pedicle opening was small, and in *Glossia* the area was minute, and sometimes slightly anacline (beak incurved). Therefore, deeper taxa show similar adaptations, possibly because these too needed a pedicle for attachment to shells or basal skeletons, but for different reasons. Here the fixosessile mode of life was probably necessary to raise the shell above the soft muddy substrate in a subvertical position, and to elevate the lateral commissure above the mud to avoid incoming fine sedimentary particles.

Silurian *Atrypa* and *Gotatrypa* showed variable pedicle adaptations: very early neanic growth stages demonstrate a small pedicle opening, sometimes even with small, solid plates (the name '*Atrypa*', meaning 'without a hole', is somewhat of a misnomer, as most show signs of some kind of pedicle opening). In adult stages the pedicle opening and deltidial plates were lost. However, the pedicle cavity in both genera shows a thick pedicle callist, growing thicker and more prominent with age, suggesting presence of a large pedicle or pedicle tissue. In both there is also commonly the secretion of a raised pedicle collar from the callist: a pipe-like structure to which a small pedicle muscle was attached. The ventral beak of these genera shows either strong incurvature, and the absence of an area, or the inside of the ventral beak is simply pressed against the dorsal umbo (adpressed), leaving a slit-like gap between the two valves. The pedicle muscle was probably eliminated in adult stages, but the tissues that secreted the callist and collar probably continued to function under the beak. Thus the loss of a pedicle meant a liberosessile existence: this loose mode of life was compensated here by the production of frills, as the shell lay in a ventral valve down position. This mode of life was of assistance on deeper, soft muddy bottoms (e.g., Lower Visby beds, *Oglupes visbyensis*), or in shallow, sheltered habitats with soft muddy substrates (e.g., *Atrypa reticularis*, and *A. sowerbyi* in the Hemse beds, NE facies, behind the reef belt). Thus water depth was irrelevant here. In the genus *Atrypoides*, *A. sulcata* from the lower Hemse beds generally

had a small pedicle opening throughout its growth stages, as did its later counterpart, *A. hemsea*, in reefal habitats. The younger, globose species *Atrypa prunum* showed beak incurvature and covering of the pedicle opening at an early stage: adults lacked a pedicle, but the shell was umbonally heavy and maintained a subvertical mode of life, anterior commissure pointed up.

Internal structure

The internal morphology of the shell of atrypids had two main components, the hinge mechanism that enabled the shell to open and close efficiently using a set of muscles and hinge structures, and the lophophore system, supported in atrypids by a calcite framework that facilitated the filter pump. A third system was the pedicle muscle attachment to the substrate, i.e., as evident from the pedicle opening, pedicle callist, pedicle collar, and deltidial plates, discussed above. The other systems left no trace, e.g., the digestive tract, reproductive organs (except possibly gonadal imprints), and endocrinal glands.

As articulated brachiopods with an efficient ball-and-socket, cyrtomatodont hinge system, atrypids possessed a strong set of relatively widely spaced teeth in the ventral valve, which fitted into a set of closely spaced sockets located in the posterior apex of the dorsal valve. The atrypids opened their shells with the help of diductor muscles (large on the vv), and closed the shell with adductors (large on the dv): thus the opposing valves show opposing muscle scar sizes, where one set is large, the other is small. The diductors occupied a very narrow space inside the dorsal umbo: in some species the fixation site can be identified by the presence of a small, bushy, ridged–striated cardinal process (usually only 2–3 mm across) located on the inner socket ridges and spread over into the posterior-most part of the cardinal pit, a narrow slot in the plane of symmetry (Fig. 7). The presence of a cardinal process is partly age-dependent, as gerontic specimens often have them, and neanic shells usually do not. There is also considerable intrapopulation, and inter-species variation in the presence or absence of a distinct cardinal process. The adductor scars on the dorsal valve are usually kidney-shaped, and are divided into two sections, a more deeply grooved posterior, and shallower set of anterior scars.

On the opposing ventral valve, the diductors are large (one third to half shell length), and round or flabellate to hatchet-shaped, and the adductors are small, located within the postero-central part of the diductor muscle field. Muscle fields are generally impressed in the Silurian atrypids, and not raised on platforms. The amount of incision is not only variable between groups but even within species. Atrypinae generally have well-developed muscle traces, but other groups, e.g., Spirigerinae, Plectatrypinae, Atrypinae, with thinner shell walls, usually had only weakly impressed scars. The smaller the shell, generally the weaker the muscle field impression. The ventral valve generally shows more incised muscle scars, and vascular canals, than the dorsal valve. Within adult *Atrypa reticularis* shells, for example, muscle scars vary by as much as 50% in terms of the shell floor space they occupy, or within the amount of incision into the shell, and the infraspecific shape variation of the muscle

field is very large (see *Atrypa reticularis* and *A. sowerbyi*). This made the size and shape of muscle scars of little taxonomic value.

Using serial sectioning techniques, the nature of the tooth–socket mechanism, and the nature of the brachidium (crura, spiralia, jugal processes), became readily apparent within each genus. Each genus carried its own distinctive pattern and design. The opening and closing of the shell is evidently closely related to the nature of the lophophore, since the lophophore can only function when the shell is open, and must shut down its pumping operation when the shell closes.

The teeth in the ventral valve possessed either dental cavities (e.g., large in *Septatrypa*, smaller in *Eospinatrypa*), dental nuclei (e.g., slit-like in *Spirigerina*, or concentric in *Gotatrypa*), or were solid, without either nuclei or cavities (e.g., in *Atrypa*, seen in Fig. 8). These hinge features appear to be consistently diagnostic within all atrypid groups, and to show evolutionary trends from group to group, or genus to genus. Silurian *Atrypa* appear to have a dental nucleus in very early growth stages (sometimes even dental cavities in neanic shells less than 5 mm wide), and to have lost these in some adult shells. The thickness of teeth and hinge plates were not necessarily coupled into adaptations of higher energy: *Oglupes muldea*, for example, is a deeper water dweller, but has relatively thick and strong teeth. *Spirigerina* was a reef dweller in the Wenlock, and also had a relatively thick shell wall and strong teeth. *Septatrypa* was a biostrome dweller of coral thickets, and lived in a more sheltered or deeper habitat: it had very large dental cavities, delicate teeth, and slender hinge plates. *Atrypa* had solid teeth, and lived in onshore, back-reef, and reefal environments: the teeth were about the same in both higher energy reefal and sheltered back-reef dwellers. Thus the possession of a specific type of hinge in atrypids is more of a genetic (genotypic) rather than ecologic (phenotypic) variable.

The crura served as the attachment points for the spiralia, i.e., the support of the lophophore. Crura were projected from the inner side of the socket plate, and the inner and upper margins of the cardinal pit. They are clearly seen to be extensions of the fine, secondary fibrous layer of the socket plates, i.e., the plates that line the socket. The posterior origins of the crura, i.e., the crural bases, do not quite meet at the apex of the cardinal pit, but can be traced to just on either side of the cardinal pit. From their point of attachment on the hinge plate, the two crura radiate at an angle towards the side of the shell, usually at a sharp angle of almost 90°, and frequently became fibrous or bushy, instead of a solid plate or rod. In cross-section, the crura are round, and do not form crural plates, as seen in the athyridids and spiriferids. The other spire-bearing groups are also not known to have produced such bushy crural fibres. Many taxa have a notch on the inside of the teeth that accommodates the passage of the crura, perhaps restraining its movement and providing some support (e.g., as seen in *Spirigerina marginalis*). The development of crural fibres is a late evolutionary trend that is independently seen in both the Lissatrypidina and Atrypidina, and started in Early Silurian time. Some atrypids appear to lack a direct and continuous connection to the junction of the spiralia lamellae and jugal plates, but a direct connection is known for most Ordovician taxa. Samtleben (1972, 1975) has pointed out that in Permian athyridids

Fig. 7. Adductor, diductor, and pedicle muscle systems. (a) Dorsal valve with hinge plate and adductor scars, cardinal process lacking, *Oglupes muldea*, Br42475, $\times 2$; (b) dorsal hinge plate with double set of adductors scars, lacking cardinal process, *Oglupes muldea*, Br42476, $\times 2$; (c) ventral valve with pedicle callist, broad diductor scars, and small, reniform adductors, *Oglupes muldea*, Br42477, $\times 5$; (d) dorsal valve showing small cardinal process, adductors, *Atrypa (Atrypa) slitea*, Br107899, $\times 6$; (e) ventral valve with large, round diductors, *Atrypa (Atrypa) reticularis*, $\times 2$; (f) ventral spatulate diductors, and small round central adductors, *Spirigerina marginalis*, $\times 4$; (g) detail of pedicle callist and pedicle collar, *Oglupes muldea*, Br106536, $\times 10$.

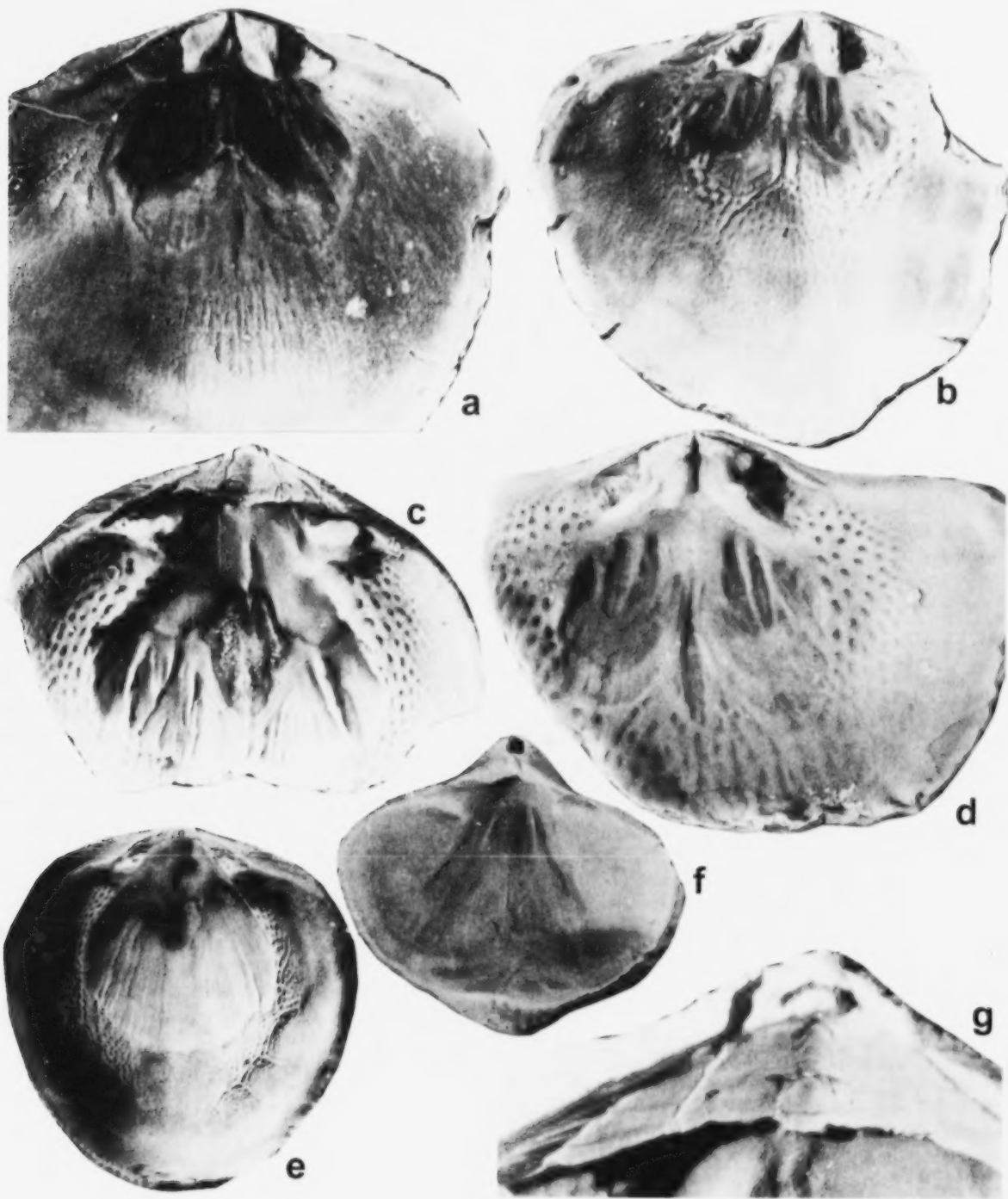
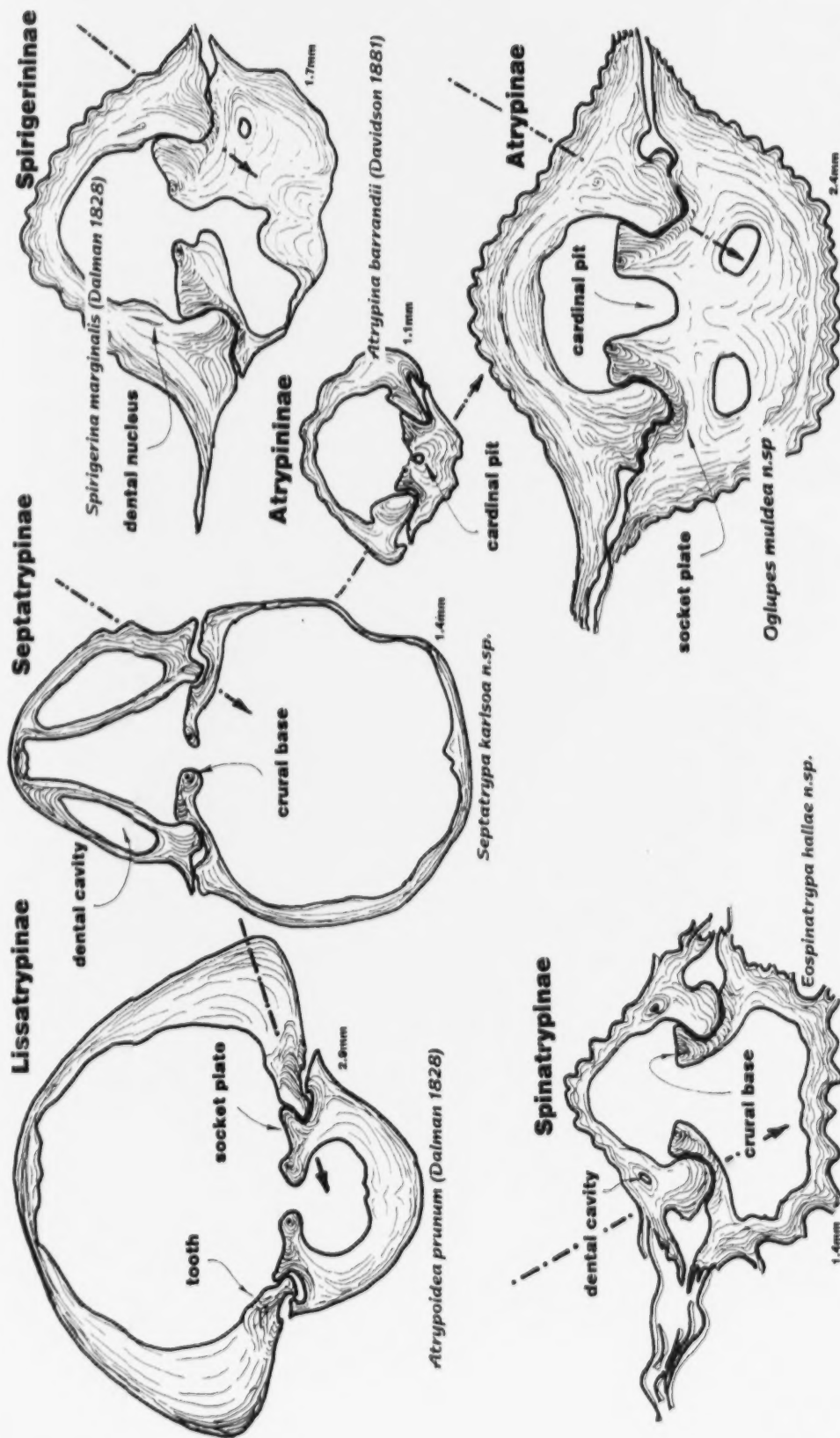


Fig. 8. Tooth and socket mechanisms in six atrypid subfamilies. All serial sections taken through middle of tooth to show the fit of teeth and socket plates of Gotland atrypids, with arrows to indicate the direction and angle of tooth emplacement. Note that there are concrete differences in the strength of the hinge plate between subfamilies: the socket plate is only the inner part of the hinge plate accommodating the tooth [distance in mm from ventral apex, ventral valve up, all at ca. $\times 6.7$].



and spiriferids the direction of growth of crural fibres is in direct opposition to that of the fibres in the spiralia, and that the junction between crura and spiralia mark a critical point. This suggests that the spiralia grew towards the crura, and that the oldest part of the spirarium is the apex, with continual secretion and matching resorption of the fibres during growth occurring in the area around the junction with the crura. This theory was disputed by MacKinnon (1991), who suggested continuous resorption during life, and that the spirarium apex was the youngest calcite secreted. The nature of this crura-spiralia suture is still not very clear for many atrypids, requiring well-preserved and exposed spiralia.

In atrypids the crura lead to the spiralia and jugal processes at a critical triple junction near the postero-lateral shell. From here, the jugal processes in most Silurian Atrypida are directed to the middle of the shell, near the plane of symmetry, with the exception of the last Anazygidina, which have a jugum [e.g., *Zygatrypa exigua*]. The jugal processes are posterior to the spiralia, and curve around in the plane of symmetry at an angle commonly almost 180°, almost back to the sides. Many taxa have nodes and very short spines at their jugal terminations. This curvature, almost like the crook of a walking stick, is evident in nearly all of the serial sections, and can be seen in the reconstructions of the brachidia for most species. The jugal processes terminate in another set of small or large plates called the jugal plates: these plates may be hook-like, spatulate, blocky, or simple small and slender boomerang-shaped structures. In *Lissatrypa* the jugal plates may form a ring-like structure at the end [see *Lissatrypa obovata* (Sowerby, 1839)], which is characteristic of most species in the genus. The jugal processes are normally in a very posterior position, behind the spiralia, and are, in Silurian atrypids, more ventral than dorsal in location. Only in the primitive genus *Zygatrypa* is the jugum dorsal to central in position. The migration of the jugum and evolution of separated jugal processes is a major development in the order Atrypida (Copper and Gourvennec, 1996). That the jugal processes were separated by a gap was first discovered by Ginley (1878); nearly all later workers ignored this evolutionary change from a jugum to separated jugal processes in the suborders Atrypidina, Lissatrypidina, and Davidsoniida. This feature was only re-confirmed much later by the detailed study of Alekseeva (1960b).

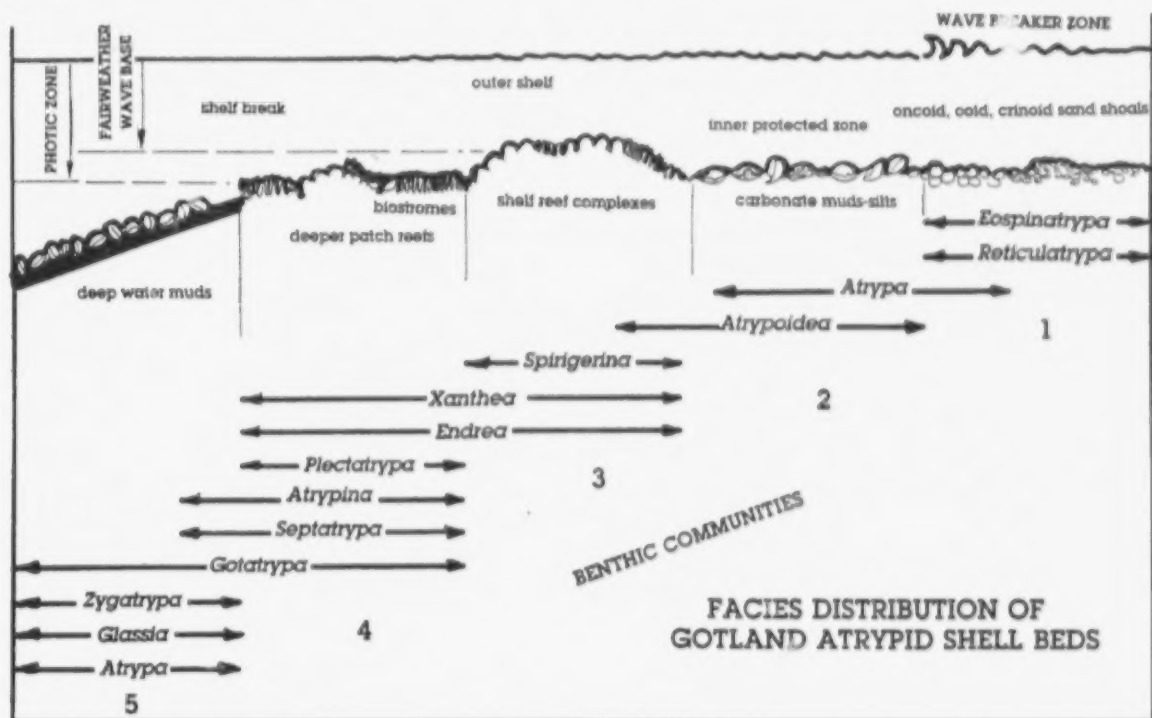
The spiralia of the Silurian atrypids examined follow three trends: (1) mediadorsally directed as in primitive *Zygatrypa*, (2) medially directed as in *Glassia*, and (3) dorsally to dorsomedially directed as in most other genera. The number of spiral whorls is partly a factor of size: smaller neanic shells, and smaller adult genera, have fewer whorls, thus a factor of ontogeny or phylogeny. The width of the spiral whorl is greater in more 'advanced' genera (those which appeared later in the fossil record), but may also be a factor of size, with large shells of large *Atrypa*, for example, having wider whorls at the base of the spirarium. It has been argued by MacKinnon (1991) that there is accretion-resorption of secondary fibres, producing a wider whorl with age, and that the youngest, or last produced whorl is at the apex, like the conical apex of a Christmas tree. Conversely, it could be argued that the first produced (and oldest) whorl is at the apex, with the shell successively pushing the preceding whorls towards the apex, in what has been called the 'corkscrew' system, and that

there is continuous secretion of the whorl at its base (Samtleben, 1972, 1975). The Samtleben model is probably the simplest solution, requiring the least amount of resorption energy for the production of calcite lamellae, especially in early spirarium growth when the shell was small and spirals were circular in plan view. The apical whorls are nearly circular in plan view, and the basal, widest whorls are often D-shaped in large shells of *Atrypa*. This requires constant resorption in adult shells, whichever model is preferred. In *Gotatrypa* the spirals appear to have remained circular at all growth stages, largely eliminating the need for resorption, if the 'corkscrew' system applied. In larger shells, e.g., of *Gotatrypa*, *Oglupes*, or *Atrypa*, that could reach widths of more than 30–35 mm, the spiralia tend to take up most of the interior shell space. In order to expand, the conical whorls 'competed' for space, and, being mirror images of each other, would have a straight inner side. Davidson already illustrated such D-shaped spiralia in 1853. Notably, however, the smaller taxa such as *Spirigerina*, *Plectatrypa*, and *Atrypina* have almost perfect spiralia cones, and lack this D-shape in adult shells. Large shells of 'sophisticated' genera such as *Atrypa* have a considerable overlap of the spiral lamellae, when one views these in a dorsal direction: smaller genera such as *Xanthea* lack this overlap. It seems possible that there was a broad trend towards enlargement of the spiralia alongside shell size increase. This was evident in the Atrypinae in the Silurian, but in the Spinatrypinae and Variatrypinae only in the Devonian. This may have improved the efficacy of the lophophore filter pump. A bigger pump presumably led to a larger nutrient uptake, with the first trends in this appearing in the later Llandovery with such taxa as *Oglupes visbyensis*, one of the largest shells, with the greatest number of spiralia whorls of its day.

Paleoecology and habitats

Atrypid brachiopods from northwestern Europe occupied a range of settings from shallow onshore, marginal marine facies with gravels of calcimicrobial oncoids (e.g., *Rothpletzella*), to deeper lagoonal or back-reef quiet water regimes, to shallower reefal habitats in mid-shelf to shelf edge environments, to deeper water, offshore conditions (Fig. 9). Atrypids were absent in foreshore siliciclastic regimes, e.g., the uppermost Slite siltstone or the Burgsvik beds, except in rare lenses or thin layers, where they were primarily reworked, and possibly storm deposited. In general, the same pattern of facies distribution applies to atrypid species as it did for broad facies patterns in the Gotland section, e.g., as seen in Hede (1960), and Samtleben et al. (2000) for the Gotland Ludlow, and in the carbonate shelf of the Wenlock in Britain (Corfield et al., 1992). There is no readily discernible Gotland pattern of onshore shallow marine to offshore deeper marine assemblages, as clearly pictured for the Llandovery by Ziegler (1965), Cocks (1967), Ziegler et al. (1968), and more recently Watkins (1979) and Watkins et al. (2000) as benthic assemblages 1–5 (BA-1 shallowest to BA-5 deepest). Such water depth patterns are possibly more applicable to ramp settings than to carbonate platforms. Some of the Early Silurian key biota had also largely vanished by the middle Silurian (e.g., *Eocoelia*, *Pentamerus*, *Stricklandia*, etc.), and keystone taxa were replaced. On a carbonate platform, a

Fig. 9. Atrypid benthic assemblages identifying the primary occurrences of genera in a shelf transect. Approximate widths of these carbonate biotopes was from 20 to 40 km, and water depths probably ranged from below the normal photic zone, e.g., 30–100 m (no. 5), to shallowest (no. 1) of less than 5 m depth subtidally. The genus *Atrypa* had a split distribution, and tended to prefer sheltered muddy substrates, either in deeper or in shallower waters. Other genera ranged across a variety of substrates but less commonly intersected more than one setting. These 'benthic assemblages' (BA's) do not necessarily correspond to siliciclastic ramp communities as used for the British Llandovery–Wenlock–Ludlow (e.g., Ziegler, 1964; Hancock et al., 1974). Atrypids were not adapted to the intertidal zone.



'shallow water' community can appear at the shelf margin, tens to a hundred or more kilometres offshore, and a relatively 'deeper water' (back reef or lagoonal, or atoll lagoon, 50–100 m deep) community may be closer to shore. For the Wenlock and Ludlow on Gotland only a small percentage of outcrops can be identified for settings as deep or deeper than BA-4–5 (as for the Llandovery *Stricklandia* BA-4 and *Clorinda* BA-5 assemblages), or at best from 'shallower' to 'deeper'. This applies especially to genera such as *Atrypa*, which range from about the *Stricklandia* BA-4 equivalents, e.g., the deeper Slite or Klinteberg facies, to almost the intertidal, possibly (*Lingula*) BA-1 equivalents in the oncoid Eke facies. There was probably a very sharp shelf edge break at the margin of the Klinteberg reef facies and the slope deposits to the west, as the two facies have almost no brachiopods in common within a distance of 1–2 km. The specific water depth is difficult to determine and at best approximated in relation to other shallow water criteria such as the presence of red and green algae, corals, and wave energy proxies.

A recent retrospective on water depths for Silurian benthic communities was carried out by Brett et al. (1993). They suggested, using cyclocrinoid algae, borings, and corals as indicators, that Llandovery BA-1–BA-4 were in water depths confined to the normal photic zone at <40–60 m, compressing their range to relatively shallow shelf or ramp areas.

Zooxanthellate corals may form reefs in very clear waters at depths today of up to 1200 m off the Florida Shelf (Robert Halley, personal communication). This implies that corals can flourish at depths greater than normally visualized. Most atrypids are found in settings where colonial corals are common, although in the deeper water assemblages such corals may be very small to absent (e.g., the *Glossia* setting in the Mulde Marl).

Calculations of water depths are speculative. It is almost impossible to say, for example, if the lower Hemse species *Atrypa reticularis*, sensu stricto, came from a BA-1 or BA-2 setting or even a BA-3 inter-biostromal facies. On the facies map of Samtleben et al. (2000, fig. 2), *A. reticularis* s.s. was present only in a marginal marine setting, i.e., about BA-1 (or BA-2), and probably correctly estimated! However, *Atrypa* sensu lato occurred from the equivalents of about BA-4 in the Upper Visby beds, through the distal shelf, reef belts, back reef, and proximal shelf over a carbonate platform from 60 to 80 km wide. Thus *Atrypa* could occur in shallow waters at 40–60 km from the shoreline, but still be in deeper waters closer to shore (Fig. 9). In such instances, water depths, distance from paleoshore, and brachiopod distribution become relatively immaterial. This makes it very difficult to assign a benthic assemblage number to any fossil occurrence for the Wenlock and Ludlow of Gotland and

Britain, a problem comparable to assigning communities to carbonate platforms of the Great Barrier Reef today. In the Ludlow, most British occurrences of atrypids were in deeper waters. In Gotland, Ludlow occurrences span shallower ends of the spectrum. Generally, Wenlock and Ludlow *Atrypa* have been broadly assigned to a BA-3 'depth community' by most workers, i.e., of intermediate or mid-ramp depth (Boucot, 1975; Watkins, 1979; Musteikis, 1991; Musteikis and Juskute, 1999). However, for atrypids there is no apparent direct connection between water depth and its occurrence, i.e., they did not respond in their location to water depth, and concomitant factors such as light (there is no reason to assume they had photosymbionts), and water pressure. Location below or above wave or storm base was possibly a factor in relation to energy during life and transport after death. Atrypids were stationary, and adapted primarily to the soft, firm, or hard nature of the substrate (immaterial to depth), grain size of the sediments, availability of attachment sites (clasts, shells, hardgrounds, dead or live corals, or sponges, etc.), bottom energy at the sediment-water interface, water turbidity, prevalence of mobile burrowers or bulldozers, and possible nutrient supply (for the last there is no criterion to distinguish quantitatively). These are the same factors used by sedimentologists and coral, sponge, and reef workers to distinguish carbonate facies, and it is in this light, i.e., the carbonate substrate, that atrypid distributions were studied.

Brett and Baird (1995) used a modified version of the benthic assemblage model of Ziegler (1965) and Boucot (1975) to analyse Siluro-Devonian communities of the eastern U.S. They suggested, as have others, that such communities were stable over very long periods of time, and thus settled into 'coordinated stasis', with similar species living in tandem, or living as 'Ecologic Evolutionary Units' [EEUs]. In practice, the 'coordinated stasis' viewpoint is the same as the BA concept, i.e., relatively long-lasting communities identified by key taxa. There seems to be neither an '*Atrypa reticularis*' nor '*Atrypa*' community (nor *Atrypoidea*, *Plectatrypa*, *Septatrypa* community, etc.) that was stable for any length of time, and thus neither the term stasis nor Ecologic Evolutionary Unit seems applicable for constant evolutionary change and shifts in communities through either the British or Gotland sequence. Atrypids probably fitted into whatever niche was dictated by stochastic larval settlement, on a substrate where the adult shell could survive. At times atrypids were rare components, at others they formed 50% or more of the shelly population. *Atrypa gotha* occurred as a very rare component in and around the Upper Visby patch reefs, probably in mid- to distal shelf settings (BA-3-4?). *Atrypa slitea*, for example, was most common in the middle to upper Slite NE proximal shelf facies belt (BA-2-3?). *Atrypa muchisoni* was present in the distal shelf setting on the SW side of the Hemse belt (BA-2-4?), whereas *Atrypa reticularis* s.s. occurred in the NE marginal marine Hemse carbonate facies some 40-50 km closer to the paleoshore (BA-1?). *Atrypa reticularis* is occurred rarely with *Atrypoidea*, and commonly with *Protochonetes* and *Didymothyris*, but where the latter two were abundant a few centimetres above or below, *Atrypa* was rare. *Atrypa alata* was located in the SW part of the Eke oncoidal facies belt (BA-1-2?), but absent in shelly-coralline facies, where *Endrea ekenia* was located (BA-2-3?). Thus one could assume rapid and random

oscillation of a number of shelly communities through various carbonate cycles, sometimes of several assemblages of shells within less than 1-2 m of stratal thickness, without any change in water depth. This is the same reason why carbonate petrologists do not use benthic assemblages to estimate relative water depth. In carbonate shelf and ramp settings, sediment is nearly entirely internally derived and thus produced in situ, very different from a siliciclastic model, dependant on proximal to distal sediment supply. In carbonate platforms, depth plays no major role except below ca. 30-100 m, or the platform break, where carbonate production and coral algal growth drops off rapidly with loss of light.

During their evolution, a number of genera migrated and evolved from deeper distal shelf to slope environments (e.g., *Plectatrypa*) to peri-reefal regions (e.g., *Xanthea*). This example was repeated in *Atrypa*, one branch of which, *Endrea*, migrated to peri-reefal and reefal substrates during the Wenlock, although *Atrypa* itself maintained both a deeper to mid-shelf setting. This shift in habitats from deeper water in the Llandovery to shallower in the Wenlock and Ludlow is a general trend reflected in many Silurian atrypid subfamilies, and probably has much to do with global changes in sea level during the latest Llandovery and Wenlock, which also stimulated widespread, nearly worldwide growth of reefs at the time. The converse, migration from shallower to deeper, possibly applies to the evolution of *Eospinatrypa*, the earliest, Wenlock, which appeared first in a shallow water, oolitic, shoal to perireefal biotope, and which only in the Devonian are more common in deeper waters. Jablonski et al. (1983) and Sepkoski (1991) have suggested that during the Phanerozoic the general pattern was that shelf communities spread from shallow onshore habitats to deeper shelf areas. This may be appropriate for lingulids (which were evolutionarily stable), and middle Paleozoic bivalves and gastropods (which certainly favoured shore-fringing, sandy substrates), but appears not to be the pattern for many brachiopod taxa in tropical carbonate settings, especially the spire-bearers, pentamerids, and rhynchonellids. The onshore-offshore migration pattern is also clouded by the possibility that cooler water Gondwana-Malvinokaffric brachiopods migrated into tropical regions, after times of global cooling and sea-level fall when the tropical biota suffered. Extinctions of tropical taxa during global cooling phases obscure the patterns of shelf extinctions, as sea-level drop would affect the reefal taxa more than deeper water forms. Since the climatic regime and paleogeographic distribution of brachiopod genera is almost never recorded, nor analysed, a 50-50 distribution of deeper-shallower water, colder-warmer taxa would override any general trends. On Anticosti Island, for example, the *Pentamerus* lineage started with in situ shell beds in a deeper, distal shelf setting in the Gun River and lower Jupiter formations (Aeronian), then migrated to a shallower setting in the Telychian, but disappeared at the crinoid shoal, reefal and peri-reefal communities (Jin and Copper, 2000).

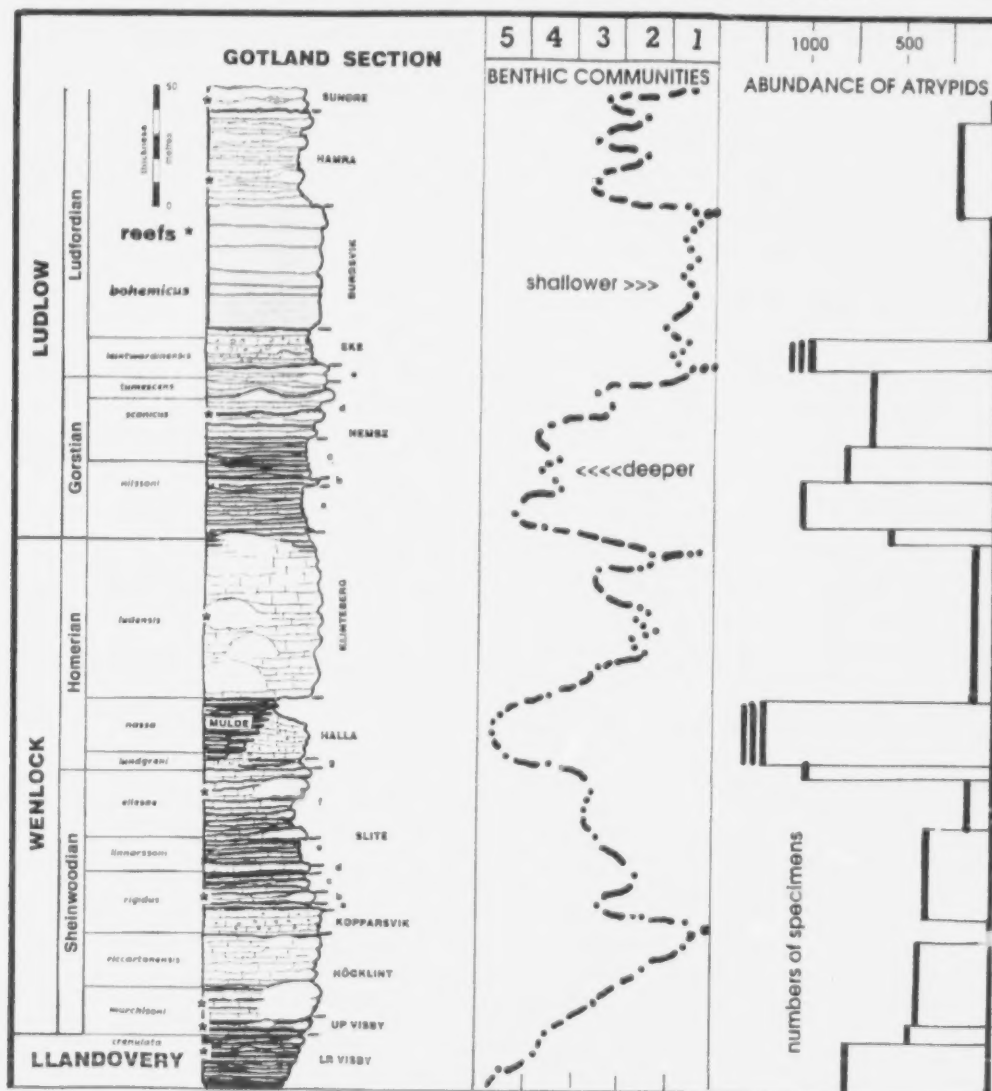
Radiation and extinction signatures

It appears to be generally more difficult to define specific diversity and evolutionary events for Silurian atrypid brachiopods of NW Europe, than it is for suggested expansions, radiations, declines, and extinctions in other groups of fos-

sils. For the nekto-planktic conodonts, Aldridge (1975), Jeppsson (1987), and Aldridge et al. (1993) discussed an early Wenlock extinction event at the end of the *Pterospirifer* *amorphognathoides* Conodont Zone, below the top of the Lower Visby shales, i.e., prior to the *centrifugus* Graptolite Zone. This was said to coincide with a change from oxygenated to greenhouse conditions, and regression. Jaeger (1991) similarly discussed marked changes in the planktic graptolites at the top of the *ludensis* Zone, around the Wenlock–Ludlow boundary. There are no clear correlations between these Wenlock–Ludlow planktic events and the first appearances or final losses of benthic atrypids. This may be related to the substrate specific nature of pedicle attached or libero-sessile taxa such as brachiopods. Nevertheless, it is relatively easy to correlate atrypid species from Gotland to Britain, provided the appropriate facies occur (Fig. 10). How did atrypid abundance and diversity relate to events predicted by stable isotopic signatures? Jux and Steuber (1992) recorded a rapid rise in δC^{13} from the Visby through Höglint strata (probably including the Kopparsvik Fm.), then a dramatic drop in δC^{13} to negative values at the top of this level, with a recovery beginning at the base of the Slite and continuing rise in δC^{13} to returned high levels in the early Hamra beds. Jux and Steuber (1992) interpreted their Gotland isotopic curves in terms of sea-level change and crustal behaviour of the Caledonides to the north and west. Wenzel and Joachimski (1996) showed a similar rise in δC^{13} (and δO^{18}) from the Lower Visby through Höglint beds, then a decline bottoming out in the middle Slite, rising through the Klinteberg and falling in the Ludlow (Hemse beds), with a final sharp rise in the Eke beds. They attributed δC^{13} and δO^{18} isotope values to global sea-level lowstands and colder waters, and light values to highstands with warm, stratified, shallow saline waters. Bickert et al. (1997) repeated the sample procedure of the preceding, but came to very different interpretations of essentially identical isotopic curves. Samtleben et al. (2000), expanding the work of Bickert et al. (1997), discussed the Ludlow part of the Gotland section in terms of platform habitats, their δC^{13} ratios showing late Wenlock peaks in the Mulde beds, a drop in the Hemse, and subsequent sharp rise in the Eke–Burgsvik strata. The last two papers related Gotland isotopic signals to fluxes between humid climates, with estuarine, eutrophic waters (light isotopic values), and heavy signals during arid periods of anti-estuarine circulation, combined with oligotrophic and saline waters (comparable to the Jeppsson 1990 model). This meant that the last two papers considered that reef abundance was tied to sea-level lowstands and high salinities, in general, contradicting global Phanerozoic patterns of reef distribution. Reefs normally reach their peaks during transgressive highstand systems tracts providing abundant accommodation space for reef expansion (Kiessling et al., 2000, 2002). At present it seems difficult to match such stable isotope data closely to the record of abundance, diversification, and losses in atrypid brachiopod species, and to reef growth. Jux and Steuber (1992), Wenzel and Joachimski (1996), and Bickert et al. (1997) all recorded sharp negative δO^{18} and δC^{13} values for the top of the reefal, and inter-reefal Höglint. This was a period of shallowing, regressions, and hiatuses (Watt, 1988; Riding and Watts, 1991). Regional lowstands appear to have had little effect on the atrypids, which continued a

steady species march across the inner and middle shelf on Gotland during deposition of the Höglint, Kopparsvik, and Slite carbonates. However, in the Anglo-Welsh Basin, atrypids generally retreated and declined in diversity and abundance during deposition of the Coalbrookdale strata (from the Wenlockian *riccartonensis* through *lundgreni* zones), perhaps in response to down-warping of the basin, and higher rates of sedimentation. A second positive set of excursions from the Eke through Hamra beds, also marked by shallowing episodes (Cherns, 1982), occurred during a general decline of atrypids in Gotland. However, in the Estonian and Lithuanian part of the Baltic Basin, the same genera and communities, e.g., *Atrypoides*, *Atrypina*, *Atrypa*, etc., continued without a break into the Pridolian (Musteikis and Paskevicius, 1999). Thus atrypids shifted with facies, but were not marked by extinctions, only loss of habitat. Atrypids could generally survive in deeper waters, but turbidity, high suspended mud content, and fluctuating, unstable substrates may have had an impact on these complex suspension feeders with spiral lophophores. The Estonian isotopic record (Kaljo et al., 1997) shows an early Wenlock, ca. Höglint peak in Estonia similar to that of Gotland. However, the Estonian curve is at variance with the Gotland data in that it misses the isotopic excursions of the later Ludlow (Eke equivalents), and shows a δC^{13} peak in the Klinteberg reefal equivalents on Gotland, matched by an only weakly positive excursion in Britain (Corfield et al., 1992) and Gotland (Wenzel and Joachimski, 1996). A sharp depletion of δC^{13} in the 1–2 m thick *nassa* Zone of the type Wenlock shales in Britain (Corfield et al., 1992) is not recorded in the equivalent lower Mulde beds of Gotland (Wenzel and Joachimski, 1996). The British signals at the top of the Wenlock are ambivalent, with some sections (Ludlow, Malverns, Denby) showing a drop in δC^{13} , and others none (Wenlock Edge, Builth). The δC^{13} drop on Gotland occurs at the end of the *nilssoni* Zone, in the lower Eltonian, and not at the end of the Wenlock (Wenzel and Joachimski, 1996). It is possible that some of these isotopic differences recorded in Britain, Gotland, and Estonia are related to sampling problems. Shells examined for their isotopic signals ranged across environments, including very shallow (Eke beds) to deep (Lower Visby and Mulde beds), and their isotopic signals may have varied accordingly from warmer, shallower waters to deeper, cooler waters, or to circulation and sediment input variables of the Baltic Basin. Climates may also be regionally very variable within a short distance in the tropical belts. For example, at 5°–10°S latitude in Indonesia today, the humid monsoonal belt of Sumatra and Java through Bali and western Lombok (with a SE Asia flora) changes eastward to the climatically more arid belt of Sumbawa, Sumba, and Timor (with an Australian flora). Reefs occur there in nearly all the open marine shelf areas, and the Wallace Line runs between Bali and Lombok, marking a geographic break, but partly also a humid-arid climatic break. In the semi-enclosed epicontinental, equatorial Java Sea, with lowered, quasi-estuarine salinities and high riverine sediment and nutrient input from Borneo (Kalimantan) and Java, reefs are poorly developed in humid settings (Edinger et al., 2002). The equatorial belt to ca. 8°S is notably also devoid of monsoonal typhoons, that might produce bottom advection. The Baltic Basin lay in roughly 20°S lati-

Fig. 10. Trends of shallowing and deepening in the five atrypid benthic assemblages of Gotland (with the addition of abundance data for *Atrypa lapworthi* and *A. murchisoni* from the lower Elton beds on the *nilssoni* Zone, Ludlow). The number of specimens exceeds 1500 for the Mulde and Eke beds; this is shown in a barred line. Note that abundance increases with depth in the deepest facies, but that species diversity increases with shallowing during the expansion of reefal facies (see preceding Fig. 9).



tude, on the eastern side of Laurussia; this placed it in the path of the normal tropical, high-energy storm and typhoon belt, similar to the modern Caribbean, and outside the equatorial doldrums. Thus faunal and isotopic signatures in the Baltic Basin may have a strong regional imprint. It is difficult to understand how climatic aridity and humidity can be a global factor in carbonate platforms separated by large oceans, as suggested by Jeppsson (1990) and Bickert et al. (1997). It is suggested that some of the isotopic and conodont-graptolite "events" mark diachronous boundaries produced at sea-level lowstands, e.g., at the Wenlock-Ludlow boundary. Abundance of atrypid specimens is generally biased towards deeper facies, but there are exceptions in the shallower facies of the Eke beds. In terms of diversity, greater numbers of species occur in reefal facies. For the

atrypids, there is a disappearance across the Wenlock-Ludlow boundary in the NE, but in the southwest deeper water facies the Klinteberg is already in "Hemse facies" at this time and the boundary is transitional. The Wenlock-Ludlow (W-L), or within Klinteberg boundary on the NE, and post-Klinteberg facies in the SW of Gotland, shows a small negative δO^{18} , a positive δC^{13} excursion, and lower trace element values on Gotland (Jux and Steuber, 1992; Wenzel and Joachimski, 1996). From Slite through Klinteberg facies, a general rise, then from Hemse into Burgsvik strata a drop in the sea-level curve has been postulated (Vail et al., 1977; Harland et al., 1989). The average rise in δC^{13} values, nevertheless, continues from the Slite through Burgsvik, with only minor fluctuations across the Wenlock-Ludlow transition. What this means is debatable. In the SE, i.e., the Lithuanian part

of the Baltic Basin (Brazauskas and Musteikis, 1991), the W-L boundary marked the initiation of a diachronous trend along an environmental gradient that apparently was continued from the earlier *nassa-ludensis* zones. On Gotland, diversity decreased at the base of, or within the *ludensis* Zone, noted by the loss of *Eospinatrypa*, *Plectatrypa*, and *Glassia*, perhaps a factor related to local reef buildup to which these taxa were not adapted. Lithuania shows a decrease in diversity and abundance across the W-L boundary, supposedly due to the arrival of siliciclastics from the west, which suppressed carbonate productivity in Lithuania (Musteikis and Juskute, 1999; Musteikis and Paskevicius, 1999). If these sediments arrived from the west at the time, they must have bypassed Gotland, where, however, diversity was maintained from the Klinteberg facies, and carbonate productivity continued across the boundary. Reefs again became prominent in the *scanicus-tumescens* zones of the higher Hemse beds. Only during deposition of the Burgsvik sands did Gotland receive substantial amounts of siliciclastics, suppressing the carbonate factory. This was well into later Ludlow, i.e., post-Leintwardinian time. Jeppsson (1987) identified several other oscillations in sea level, based on marl and limestone facies for the Gotland section, recording transgressive pulses within the lower Slite beds, lower Hemse beds (but not lowest), and late Hemse beds. Regressions were noted for the Upper Visby through Tofta (Kopparsvik), top of the Slite, the Klinteberg, middle Hemse, early Eke, top of the Burgsvik, and the Sundre beds. These trends roughly parallel the data provided by the shift of atrypid communities with the advance and retreat of reefal and muddy facies in Wenlock and Ludlow time (Fig. 2).

Rates of evolution for species are possible to calculate only in a rough way. For *Atrypa*, which may here be subdivided into nine species from the late Telychian through late Ludlow (ca. 12 myr long), evolutionary rates averaged to 1.33 myr per species, but some species had a long duration, and others were so scarce as to make identification and range problematic. For the reefal and peri-reefal genus *Spirigerina* (latest Wenlock through late Ludlow, ca. 6 myr), there were three species with an average duration of ca. 2 myr. *Atrypoidea* had three species over a duration of ca. 5 myr, but disappeared from Gotland because of facies changes, so that its termination is not clear.

Comparative faunal provinces

The Gotland and British atrypid faunas share a number of genera in common with those of Estonia and the remaining

Baltic Basin, Podolia, and the eastern margins of North America (Anticosti, Nova Scotia, Michigan Basin, Ontario, New York, Appalachians, etc.), especially in the Llandovery and Wenlock. Similar depth-related benthic communities occur in these regions. Thus a number of taxa which occur in the Visby beds of Gotland, and in older Llandovery strata of Norway and Britain, are shared. No detailed faunal province survey has yet been made. There are major differences, however, between the Ludlovian-Pridolian Uralian faunas and those of western Europe. The Baltic region was south of the equator at this time, on the southern flanks of Euramerica. The Ural region was north of the equator, on the northeastern flanks of Euramerica. For example, the genera *Gracianella*, *Procarinatina*, *Symmatrypa*, *Atrypinella*, *Plesicarinatina*, and *Crassatrypa*, which are widespread in the Urals (e.g., Sapelnikov et al., 1987; Sapelnikov and Mizens, 1991), appear to be absent in the Baltic, Britain, and eastern North America. A facies difference is possible, yet reefs are developed in both areas and both were in equatorial low latitudes. This suggests restricted distribution patterns relating to ocean currents. Nevertheless, the genera *Atrypa* and *Atrypoidea* are widespread in both areas. In the Late Silurian, the Uralian fauna appears to share greater similarities with those of arctic and western North America, although again the exotic Uralian genera such as *Symmatrypa* and *Plesicarinatina* are not yet reported. This distinction may disappear with further Arctic discoveries. Thus the western slope Uralian fauna may be assigned to a faunal province north of the equator, separated by surface ocean currents sweeping northwestwards from the equator to the arctic regions. Surprisingly, the Silurian faunas of the Prague Basin, ostensibly well south of the equator and on the flanks of Gondwana at the time (Golonka, 2002), share a number of atrypid genera with Gotland (Havlíček, 1998). Genera in common include *Atrypa*, *Gotatrypa*, *Oglupes*, *Eospinatrypa*, *Lissatrypa*, *Septatrypa*, and *Glassia*. The fauna of the Saxo-Thuringian micro-plate between Gotland and Prague is highly tectonised, confined to siliciclastics, and primarily restricted to graptolites (Jaeger, 1991). Plotted surface current directions for the Wenlock (Copper, 2002a) suggest that these Czech faunas were swept in counter-clockwise fashion to the southeast from Gotland and Britain.

The low-diversity faunal province covering Mongolia through the Altai carries the distinctive Wenlock-Ludlow atrypid genus *Tuvaella* (Rozman 1986, 1988), absent in Gotland, but shares the ubiquitous genera *Atrypa* and *Atrypoidea*. *Tuvaella* is a giant, remnant derivative of the anazygid *Zygatrypa* found on Gotland as late as the early Wenlock.

Systematic paleontology

Atrypoid brachiopods are a select group of spire-bearers in which the medially to dorsally directed spiral lophophore system was supported by calcite ribbons. The oldest are of late Llandeilo age, and the group became extinct near the end of the *linguiformis* Zone (uppermost Frasnian). Already in 1852, the German paleontologist Quenstedt used the term 'Calcispirae' to refer to *Atrypa reticularis* and *Atrypoides primum* from Gotland, i.e., atrypids in general at that time, but this name did not last as a general term for the atrypid group. In 1853 Davidson, rather unwillingly as seen from his text, grouped these spire-bearers under the name *Atrypa* (in general following Dalman, 1828), with ribbed forms defined as '*striatae*' and smooth forms as '*laevis*'. The order Procampyli was then later employed by Quenstedt (1882, p. 723) for both ribbed and smooth spire-bearers with dorsally directed spiralia, but this name also has fallen into disuse. In 1882 Davidson divided the spire-bearers into four families, the Spiriferidae, Nucleospiridae, Athyridae, and Atrypidae (the Nucleospiridae can be referred to the Athyridida today). However, he also included in 'those genera which have the apex of their spiral cones directed towards the bottom of the dorsal valve' (i.e., atrypoids), athyridids that are known to have laterally directed spiralia, e.g., *Coelospira* and *Anoplothecca*, and spiriferids with ventrally directed spiralia, e.g., Triassic *Koninckina*. The scheme for the taxa with dorsally directed spiralia was ultimately replaced by Rzhonsnitskaya (1960) with the order name Atrypida. More than 200 genera or subgenera have been described as atrypids in the last 100 years, and the sections from Gotland and Britain have had a significant role in our understanding of the group as a whole, not foremost because the name *Atrypa*, based on a Linnean species from Gotland, led to the name applied to the whole order. An attempt was made to catalogue the species described for different genera, but not to ascribe all synonymies, except for the species studied for NW Europe. The atrypid species are described in general evolutionary (oldest, 'primitive' early groups first), then stratigraphic sequence, with the oldest species preceding, except for the type species of the genus, where this is applicable. Classification at the subfamily and higher levels follows the newly revised brachiopod treatises (Williams et al., 2002; Copper, 2002b). Initially, on commencing this study, it was assumed that the catch-all species *Atrypa reticularis* had a long stratigraphic range, and wide shelf distribution on Gotland, following the practice of Harper (1969), Bassett and Coeks (1974), and most authors, and that the varieties described by Alexander (1949) were ecomorphs, or end-member variants of *A. reticularis*. The same assumption was followed for most other well-known described species from Gotland. This practice became untenable when important differences were recognized following the succession upward on Gotland and in Britain from the late Llandovery through Ludlow. The same species can generally be seen to appear at the same stratigraphic levels in areas, today 1300 km apart, from Gotland through the Welsh Borderlands. Large collections are required in order to understand variability within atrypid species, although many species have in fact been defined on less than 10 specimens, and often only a single specimen, or

even a single internal mould (e.g., *Atrypa plana* Sowerby 1839). In order to sort out the evolutionary and stratigraphic variables, it was decided to treat all specimens from the same genus or subgenus at any one locality, and the same stratigraphic horizon, as species population variants, i.e., assuming that all congeneric specimens on the same bedding plane, or even within the same member of the formation, belonged to a single species. Criteria to distinguish these paleontologic morphospecies were found to be variable, depending on the family level: e.g., Atrypinae may be defined not only on shape, size, and internal structure, but also on variation in surface sculpture such as ribs and growth lamellae. However, the smooth atrypids have fewer identifying surficial sculpture features, and even growth interruptions were found to be of little value in morphological identification: here shape variation was utilized. Muscle scars, gonad imprints, and vascular (pallial) canals were found to be highly variable in relief, extent, and outline within species, ranging from indistinct to highly impressed; muscle scars were thus generally discarded as usable taxonomic features. Some 58 characters were used for identifying species, genera, and families (Table 1). A general test for 'usability' of the atrypoid species was considered to be stratigraphic reliability. Thus if the same morphospecies were identified in Britain and Gotland, at the same stratigraphic level (i.e., roughly within the same or adjacent graptolite biozones), that 'species' was thought to be reasonably reliably founded. This was not always possible, as some British species were not found on Gotland, and vice versa. In part this distribution may be due to facies variation or lack of outcrop. However, old and new collections sometimes yielded surprising finds of species which were believed to be absent in either area (e.g., the common Dudley species *Atrypina harrandii* occurs eastwards in Gotland only on the small island of Utholmen). Identifying atrypoids at the species level generally required superbly preserved material with the original calcite shell: both areas showed such preservation. This preservation, plus shell abundance, also was helpful in serial sectioning. At least 50–100 specimens per species were found to be a useful number for statistical confirmation and analysis of population variation. For species of the ubiquitous, larger shelled genus *Atrypa*, even greater numbers were required for accurate identification. As a result 53 species were revised or described for the first time, some 13 000 specimens were examined, measured, and sectioned, ca. 1300 photographs taken, more than 100 specimens serially sectioned, more than 5000 Acetobutyrate peels etched and dissolved, and over 200 figures prepared. Scatter diagrams and frequency curves were prepared for species where adequate collections were available [as these were done over a period of 10 years, no computer graphics were used]. In description, the code used for the pedicle or ventral valve is vv, and for brachial or dorsal valve dv. Specimens were measured with digital or manual calipers at 0.1 mm scale for width, length, and depth, apical angles of the vv and rib spacing, where localities supplied enough specimens from the same bedding planes. For small specimens less than 15 mm wide, sample sizes of 100 were usually adequate to provide a

reasonable spectrum of size variation. For larger specimens a minimal collection was about 300–500 specimens; otherwise, frequency curves showed no averages or clusters. For materials, the locality code is cited first, followed by the number of specimens [in brackets], then the locality specifications, and the catalogue number. Primitive characters include those that are seen in the earliest genera, e.g., those

from the Ordovician: advanced characters are those which were developed at various times during the evolution of the group. Width/length and width/depth relationships are plotted on scatter diagrams, width and depth peaks on frequency curves for taxa which have sufficient material available. Species were described chronologically within genera, on the basis of older species first.

Order Atrypida Rzhonsnitskaya, 1960

[= Calcispirae Quenstedt, 1852, partim; = Procampyli Quenstedt, 1882]

Suborder Anazygidina Copper, 1996c

Family Anazygidae Davidson, 1882, in Davidson, 1883

Subfamily Anazyginae Davidson, 1882, in Davidson, 1883

Genus *Zygatrypa* Copper, 1977a

Type species. *Rhynchonella paupera* Billings 1866, Anticosti Island, E Canada, Cybèle Mbr., Jupiter Fm., late Llandovery (early Telychian).

Range and distribution. Early Silurian (Llandovery) – early Wenlock.

Diagnosis. As in Copper (1977a, p. 307–308; 2002b, p. 1440).

Remarks. This rare genus represents one of the last surviving anazygines, an ancestral subfamily of atrypids which dominated the Ordovician. Characteristic of the group is a simple jugum binding the two spiralia together, small size, strong carination, a sulcate commissure, and lack of growth lamellae or frills. Boucot, Johnson, and Zhang (1988) discovered a species from Wenlock rocks in Nevada, which would be one of the youngest horizons known. In Gotland the genus occurs as high as the early Wenlock Höglint Formation. The presence of *Zygatrypa* in Gotland would extend the geographic range of the genus beyond North America to Baltica, matching the occurrence of the catazyginid *Pentlandella* (which appears to have vanished in late Llandovery time in England and Scotland). In the Silurian, the anazyginid *Zygatrypa*, like the catazyginid *Pentlandella* (absent on Gotland, but present in Estonia), was effectively a relict, or 'living fossil', as both subfamilies are survivors of groups abundant in the Ordovician, left over from the late Ordovician extinctions. Their restricted small size may account for their lack of competitive success with much larger shells of the Atrypidae in the later Silurian. The genus on Gotland appears to have been a deep water, muddy bottom inhabitant, as seen from its scarcity in reefal beds, or beds rich in corals, stromatoporoids and calcareous algae.

Species described [in addition to Copper, 1977a].

Rhynchonella ?exigua Lindström 1861, Lower Visby beds [Ygne Mbr.], 'Skälsö', Gotland, late Llandovery.

Zygatrypa stenoparva Boucot, Johnson, and Zhang 1988, Loc. 13206, Nevada, early Wenlock.

Protozeuga carinata Rubel 1977, Estonia, drill-core material, early Wenlock [= ?*Z. exigua* Lindström 1861].

Zygatrypa exigua (Lindström, 1861)

Plate 1A, figs. a–l; Fig. 11

1861 *Rhynchonella ?exigua* Lindström, p. 366, pl. 12, figs. 7a–d.

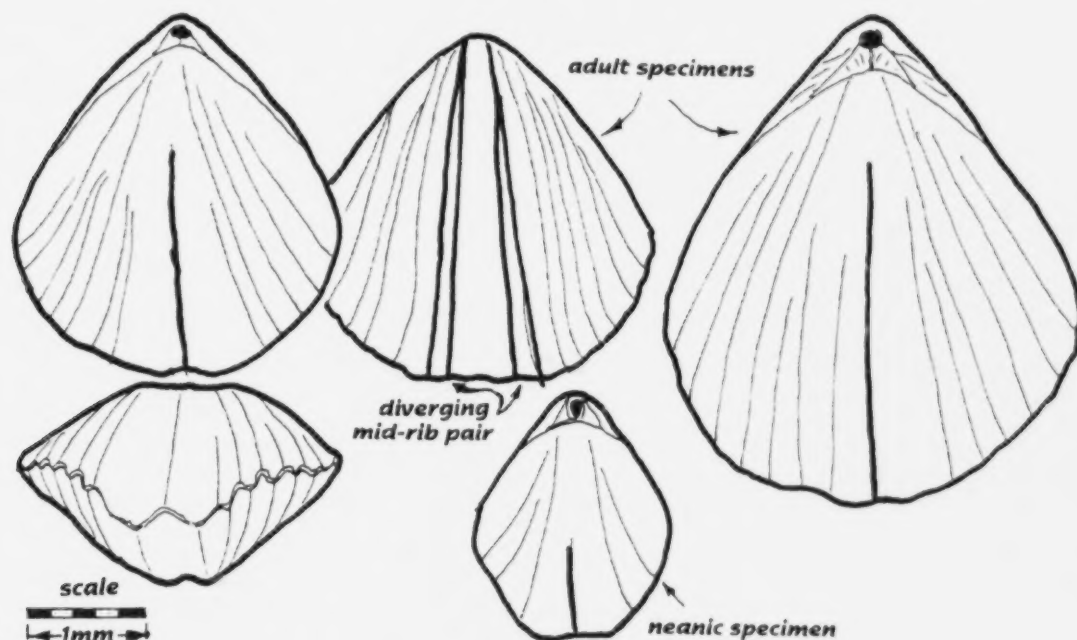
1974 '*Rhynchonella*' *exigua*, Bassett and Cocks, p. 40.

1977 ?*Protozeuga carinata* Rubel, p. 214–215, pl. 2, figs. 7–9 [tentatively classified as a dayiacean].

Type locality and stratum. The type locality is "lager vid Skälsö och Lummelund" (Lindström, 1861), on the north coast of Gotland; there are 17 syntypes in the Lindström collection from this locality. This refers to the locality known today as Själsö 1 [6 km N of the north city wall of Visby, 1 km N of the N end of the Visby airport, and 4 km due W of Väskinde; 6J Roma NV 99580:52060], where the Lower Visby shales are sporadically exposed along the beach. 'Wisby Gruppens' was indicated by Lindström (1861), more specifically in the Lower Visby beds (Llandovery–Telychian), with doubtful presence in the Upper Visby – Lower Höglint strata (early Wenlock). The type stratigraphic level is the latest Llandovery, *crenulata* Zone, but the species may range as high as the early Wenlock *murchisoni* Zone. Lundqvist et al. (1940, p. 65) cited this species also from the Upper Visby beds (i.e., lowermost Wenlock), as did Bassett (1979, p. 194), who also recorded it from the 'Upper Visby Marl' at the Vattenfallet section. The very small size of this species, at less than 4 mm width, means it is under-represented in most collections, and probably overlooked, except in microfossil collections sieved for ostracodes. Associated atrypid species include the small-shelled form *Gotatrypa hedei* Struve 1966 and large-shelled *Oglupes visbyensis*. Bassett and Cocks (1974, p. 40) cited the 17 specimens from the Lindström collection but did not select a type, and none was figured by Lindström (1861). This is corrected here with the lectotype Br102531.

Diagnosis. Shell minute, <4 mm wide, oval in outline, with narrow hinge angle, small orthocline area, apical foramen, small deltidial plates, deeply sulcate commissure. Ventral valve with two strong mid-rib pairs flanked by 5–6 fine ribs; dorsal sulcus with 1–3 ribs.

Fig. 11. *Zygatrypa exigua* (Lindström, 1861). Camera lucida drawings of three specimens, demonstrating rib structure and foramen; Lindström collection, Lectotype Br102531 is represented by the three views in the upper left corner. Själsö 1 locality, late Telychian – early Wenlock.



Description. Minute, ventribiconvex-biconvex shell, 2–4 mm wide, usually slightly longer than wide, maximum width anterior to mid-length, average thickness ca. 3 mm; outline anterior half rounded, posterior half with relatively narrow apical angle of 70° – 80° ; hinge line very narrow, pointed; carinate ventrally; ventral umbo pointed, protruding; orthocone – slightly anacline area with small apical-transapical foramen flanked by two small, transversely wrinkled deltidial plates; dorsal valve sulcus, broadly V-shaped; ribs continuous, rounded, fine, fading postero-laterally towards hinge line, with two variably strong, diverging mid-rib pairs on vv, separated by shallow groove with 1–2 fine ribs and flanked by 5–6 fine ribs, thinning laterally; dv with single strong mid-rib in sulcus flanked by 6–7 finer ribs fading away to the sides; micro-ornament of fine concentric growth filae.

Remarks. This Gotland species is one of the smallest species described for the genus to date, others being twice or more the shell width. Rubel (1977) figured a very small Wenlock species, *Cyclospira carinata*, from drill core in Estonia, which seems identical to the external morphology of the shells from Gotland, and is here interpreted as *Zygatrypa exigua*. Bassett and Cocks (1974, p. 40), following Lindström (1861), believed that *Zygatrypa exigua* was a rhynchonellid, possibly representing the type for a new genus. Nevertheless, the external morphology, i.e., carination, rib development, beak, and anterior sulcation are diagnostic of *Zygatrypa*, and although the internal shell was not serially sectioned, it is so assigned here. The shell is smaller and

more elongate than *Zygatrypa mica* (Billings, 1866), from high in the Jupiter Formation (Ferrum Mbr.) of Anticosti, to which it compares most closely. Internal structures cannot be compared with other shells, as these are still unknown. *Zygatrypa paupera* (Billings, 1866) from lower in the Jupiter Formation (Cybèle Member) is substantially larger at more than 10 mm width, more carinate, and shows rib diminution laterally. *Zygatrypa* shows progressive decrease in size through the Llandovery, until one of its last appearances in the Visby beds and early Wenlock Höglint beds.

Materials. 71 specimens, incl. lectotype Br102531. Ygne Mbr., [lower] Visby beds, Själsö 1 (= Skälsö), Lummelund, Br102531-47 [17], Lindström type collection; **Norderstrand**, Visby sn., Br57056-93 [37]; **Nyhamn 1**, Lower Visby beds, Br134653-60 [8]; **Rönnklint 1**, Lower Visby beds, Br136906-14 [9]. Lundqvist et al. (1940) cited the species from near **Nygårdsbäcken** (near Axelro), and **Brissund** (8 km N of the Visby wall) on the north coast of Gotland. Hedström (1910, p. 1469) mentioned '*Rhynchonella exigua*' in the 'Waterfall' (**Vattenfallet**) section S of Visby from 'the border strata' (unit 3), suggesting it may occur above the Ygne Mbr., and Bassett (1979, p. 194) cited it, but did not describe or figure it, from the 'Upper Visby Marl' at Vattenfallet. In addition, five specimens Br136904-5 occur in a collection labeled '**Häftingsklint**', Hangvar sn., understå Höglint. If the last is correctly identified, the species extends into the Lower Höglint, early Wenlock, on Gotland.

Suborder Atrypidina Moore, 1952
 Family Atrypidae Gill, 1871
 Superfamily Atrypoidea Schuchert and Levene, 1929
 Subfamily Atrypinae Waagen, 1883

Atrypa Dalman, 1828

Type species. *Anomia reticularis* Linnaeus 1758, lower Hemse beds, early Gorstian, Ludlow, Silurian.

Range and distribution. Late Llandovery (Telychian) through early Givetian, worldwide.

Diagnosis. Medium to large sized, dorsibiconvex to convexoplane ribbed atrypids with wavy, low amplitude ribs, weakly imbricate growth lamellae usually extended into frills, lacking a foramen or with foramen perforated into umbo, hypercline beak in adult growth stages. Internally, with large, prominent teeth normally lacking dental cavities and deltidial plates in adult stages; pedicle callist thick, infilling much of pedicle cavity; thick hinge plates; cardinal pit and inner socket ridge with or without bushy cardinal process; spiralia dorsally directed, with 6–20 whorls; jugal processes medially to ventromedially located, with short jugal plates.

Remarks. Dalman (1828, p. 102) erected the genus *Atrypa* without mentioning the dorsally directed spiralia and without designating a type species, although the first species listed later in his text (p. 127) under the name *Atrypa* was the species *Anomia reticularis* of Linnaeus (1758). King (1846, p. 29; 1850, p. 137) first officially cited the Linnaeus species as type of the genus *Atrypa*, which was followed by others later. The first illustrations of spiralia in any atrypid (for the Devonian genus *Desquamatia*) appeared in Deshayes (1827: figures of Bruguière). Quenstedt (1852) may have been the first to use spiralia to define spire-bearing groups, coining the now-abandoned term 'Calceispirae' for what are now all the spire-bearers, and later 'Procampyli' (Quenstedt, 1882) for the order Atrypida. Davidson (1853) appears to have been the first to use spiralia in a modern sense to define the various spire-bearing groups.

Atrypa is one of the most ubiquitous of all atrypid genera, having been found on every continent and in rocks from latest Llandovery to early Givetian age (earlier forms are assignable to other Atrypinae). By Givetian time it had largely given way to the related genus *Atryparia*. A number of attempts have been made to subdivide the genus or to rationalize associated genera, e.g., in Struve (1966), Copper (1966, 1973b), Rzhonsnitskaya (1975), Copper and Racheboeuf (1985), and Havlíček (1987a). The genus appears to be plastic in its evolutionary and paleoecologic variability (in terms of shape and the capacity to change its appearance by altering the nature of ribs and growth lamellae), and yet it has remained fairly conservative through its long history. Early Givetian species of *Atrypa*, for example, are similar in terms of hinge structures and brachidia to those found in Ludlow rocks.

Large numbers of specimens are required to identify and delineate species statistically. Past practice has often been to name new species, based on a single or very few broken shells or external moulds, at a rate that probably exceeds

their population variability. Most authors have thus wisely chosen to give a wide interpretation to the 'porte manteau' species, *Atrypa reticularis*, and this is reasonable practice. However, because of their great abundance locally, a number of species, as well as species-groups of *Atrypa* are useful for distant regional and even intercontinental correlation and these have been subdivided in the past into subgenera (listed below). *Atrypa* species show strong facies dependence, which makes them useful for determining shoreline relationships paleogeographically. This facies dependence does not detract from their biostratigraphic value as index fossils, once their variability and facies distribution is understood. With little practice, using blind tests, it is not that difficult to pick out the stratigraphic levels in Gotland and England from which old collections were made.

In *Atrypa*, neanic specimens <5 mm wide may feature small triangular deltidial plates, but adults lacked a functional pedicle opening. *Atrypa* is distinguished from *Protatrypa* (Boucot, Johnson, and Staton, 1964) in lacking any evidence for carination in early growth stages, and in developing frills. Internally, the differences have been clarified in that *Protatrypa* is seen to lack the pedicle callist and collar, but has dental cavities, and a very thick hinge plate without a notothyrial pit (Copper, 1995). *Gotatrypa* Struve 1966 was raised to genus status by Havlíček (1990), on the basis of 'possessing frills, or short growth lamellae', but this is a character for *Atrypa*: true *Gotatrypa* lack frills. Havlíček (1990) assigned Wenlock and younger species to *Gotatrypa*, but the Llandovery type species of *Gotatrypa* is a form that is finely ribbed, and lacks frills. Havlíček's Wenlock and younger '*Gotatrypa*' species may be assigned to *Endrea*. Many species assigned by Havlíček (1990, 1999) to *Atrypa*, which is convexoplane, are here transferred to biconvex–dorsibiconvex *Oglupes*. The genus *Endrea* (Copper, 1995) differs from *Atrypa* in having an erect beak, and deltidial plates, lacking the pedicle layer, but with dental cavities and unique micro-ornament, and short to medium frills. The genus *Oglupes* (Havlíček, 1987b) from the Prague Basin is distinct from *Atrypa* in being biconvex even in adult stages, with a weak dorsal fold, possessing coarse ribs, lacking a pedicle callist, and having a more massive dv with 'much stronger socket plates'. Gotlandian *Oglupes* have species with well-preserved frills, as well as those which appear to have gone without. Rib coarseness in Silurian *Atrypa* is great, ribs in *Gotatrypa* also appear variable in size, and strong hinges are also typical of *Atrypa*, so that the status of *Oglupes* still remains somewhat unclear (it occurs on Gotland). Specimens of the Eke species *Atrypa alata* Lindström, and older *Atrypa slitea* n. sp., show affinities with *Oglupes*, but are here retained in *Atrypa*.

Subgenera assigned. Two subgenera are identified here for Silurian–Devonian *Atrypa* (*Atrypa* and *Planatrypa*). Devonian biconvex to dorsibiconvex shells assigned to *Kyrtatrypa* Struve 1966 were probably derived directly from Ludlow or

Pridoli *Gotatrypa* or *Oglupes*. The differences between these are in part gradational, and there is probably overlap in some early species. The oldest *Atrypa* (*Atrypa*) is known from late Llandovery (late Telychian) rocks, such as the upper part of the Lower Visby beds, with the group expanding dramatically in Wenlock time. *Atrypa* may have been either derived from, or evolved contemporaneously with late Telychian *Oglupes*, both developing wide frills. The ancestral genus *Gotatrypa*, with a biconvex shell and lacking frills, preceded it in the Aeronian (middle Llandovery), the latter a bed-forming group abundant in Aeronian-Telychian rocks of Anticosti Island (E Canada). The relatively flat-shelled Rhuddanian genus *Protatrypa* (Copper, 1982, 1995) had disappeared by the Aeronian, and thus seems an unlikely precursor for *Atrypa*.

A number of related genera could arguably be assigned as subgenera of *Atrypa*, if a much broader definition of the genus is used, but these taxa have wide, time-limited stratigraphic application. Related genera include *Protatrypa* Boucot, Johnson, and Staton 1964, *Atryparia* Copper 1966, *Atryparia* (*Costatrypa*) Copper 1973, *Rugosatrypa* Rzhonsnitskaya 1975, *Peetzatrypa* Rzhonsnitskaya 1975, and *Kyrtatrypa* Struve 1966 [= *Anulatrypa* Havlíček 1987b]. There are recognizable differences in the internal and external construction of the complex shell, but the interpretation of their significance has differed substantially, as contrasted in the work of Rzhonsnitskaya (1975) and Havlíček (1987a). Havlíček (1987a) regarded *Gotatrypa* as a widespread taxon in the Silurian, but saw Devonian *Kyrtatrypa* as the intermediate between *Atrypa*, and many other Devonian *Atrypa*-like genera or subgenera. Havlíček also eliminated all use of subgenera, raising these to genus status. Most of Havlíček's species are definitively known only from their type locality in the Prague Basin, and from small, localized Barrande collections of fewer than 50 specimens. Thus infraspecific and regional variation are unknown. For example, *Anulatrypa* Havlíček 1987b is here regarded as a junior synonym of *Atrypa* (*Kyrtatrypa*), as no external nor internal differences are identifiable, unless more *Atrypa* species are raised to genus status.

Atrypa (*Atrypa*) Dalman, 1828

Type species. *Anomia reticularis reticularis* Linnaeus 1758, lower Hemse beds, early Ludlow, Silurian.

Range and distribution. Worldwide, late Llandovery (C6) – Givetian.

Diagnosis. Convexoplane to concavoconvex *Atrypa* with strongly convex brachial valve, almost planar to weakly convex to resupinate pedicle valve; beak adpressed, hypercline in mature growth stages. Ribs medium to coarse, rounded, interrupted by wave-like concentric ridges defining regular, moderately to widely spaced; concentric growth lamellae; anterior commissures in late growth stages defined by crowding and overlapping lamellae; frills, where preserved, may be very long. Internally, well-developed pedicle callist usually extending into collar; solid large teeth, normally lacking or with small dental nuclei in adult shells; massive hinge plates; crura feathered; spiralia with 6–15 whorls; jugal processes disjunct, spatulate.

Remarks. I recognize two subgenera of *Atrypa*, the Silurian forms assignable to the prominently frilled *Atrypa* Dalman 1828 sensu stricto, and Devonian species referred to as *Planatrypa* Struve 1966. Devonian *Atrypa* (*Planatrypa*) Struve 1966 have an extremely flat ventral valve, and lack any sign of frills, dental nuclei, or deltidial plates, even in neanic stages. *Atrypa* is externally distinguished from early Llandovery *Protatrypa* by its convexity and shape (see Boucot and Johnson, 1964a; Copper, 1996b). Struve (1966) described the Silurian *Atrypa* (*Atrypa*) specimens from Gotland as dorsibiconvex with a resupinate pedicle valve in late stages, concave shoulder line, weak or absent fold, moderately finely ribbed (6–9 ribs per 5 mm of arc) and especially by 'growth zones' [= growth lamellae], said to be three times wider than rib spacing. He remarked particularly on the *Desquamatia*-like resemblance of the surface sculpture. However, there is relatively little resemblance between the rhythmic waves of concentric ridges which define the breaking point of the concentric growth lamellae in the *Atrypa reticularis* group, and the tubular, interrupted ribs of typical Devonian *Desquamatia*, except in their wide spacing. The spacing of growth lamellae developed to such a stage in *Desquamatia* that only a single, continuous lamella was eventually produced around the commissure, as in the end product, Emsian to Givetian *Variatrypa*. This is completely unknown in Silurian forms.

Havlíček (1990), who examined the 50 specimens of "*Atrypa*" sensu lato from the Barrande collection in the Prague Basin, took a different view of the type species, *Atrypa reticularis* Linnaeus 1758. He interpreted such shells as being dorsibiconvex, whereas the type is convexoplane: many of the species he assigned to *Atrypa* are here relegated to *Oglupes* (see list below). Young stages of *Atrypa* are biconvex, up to a shell width of about 15–20 mm at which growth stage the anterior shell converted to being nearly flat. The development of an anterior fold or sinus is similar in *Atrypa* and *Oglupes*, i.e., it can be marked or almost absent. What sets *Atrypa* apart from *Oglupes* are convexity and the spacing of growth lamellae, and the nature of the ribs, and rib fenestrae (where preserved). The oldest *Atrypa* (*Atrypa*) sensu restricto are known only from latest Llandovery (late Telychian, C6) from Britain. On Gotland, the oldest *Atrypa* (*Atrypa*) and *Oglupes* occur in the upper part of the Lower Visby beds (Fig. 2); below this only *Gotatrypa* occurs. The development of a more planar pedicle valve, increased spacing of growth lamellae, and the early loss of a functional pedicle are typical early features of *Atrypa* evolution. These are suggested to be evolutionary accommodation to a libero-sessile mode of life, free living on a soft, muddy carbonate substrate into which the shell would otherwise sink and be smothered.

The delineation of species in the *Atrypa* group in the Silurian is somewhat more difficult than for Devonian taxa, as the first radiation of the Atrypinae was in the Llandovery–Wenlock. Distinctions between Silurian species are not always as clear as in the Devonian. There is considerable variation in frill development from species to species, and even within species from a single locality, a feature noted earlier by Alekseeva (1960a, 1968). Specimens with well-preserved frills may have quite a different appearance from those without. In part this was probably a taphonomic factor during the

lifetime of many shells. Frills appear often to have worn off during life as part of a normal growth phenomenon. This is readily seen in the distinction between young and old shells from single populations, where young shells may have frills preserved over much of the surface, but the adult shell will only show frills on the outer commissure, or perhaps no frills at all (even in well-preserved material). Considerable care must thus be taken to compensate for the evident natural loss of frills during growth, the variability in frill preservation within the same environment (shells with frills and those without in a single nest or bed), and the loss of frills due to post-mortem wear and tear.

Most paleontologists working with the '*Atrypa reticularis*' group, except for Alexander (1949), have not seen any consistent trends of stratigraphic value (e.g., Bassett and Cocks, 1974), and have accepted variation as an infraspecific response to environment. Hurst (1975, fig. 5) suggested there was a simple morphological shape variation within the community, comparing width against a width/height ratio, and he inferred that 'bulbous' varieties lived 'in deeper, quieter water'. Since no illustrations were provided, probably three genera, *Atrypa*, *Gotatrypa*, and *Endrea*, the last common in the Dudley Limestone, were present in Hurst's calculations as *A. reticularis*. This is thereby difficult to verify. On Gotland, convexoplane *Atrypa* are generally more common on the eastern side of the island (except in the very shallow Eke oncolite facies with *A. alata*), whereas the dorsibiconvex *Oglupes* species favoured deeper shaly facies (e.g., Mulde Marl, western Slite facies). There appear to be no gradations between these species-groups showing any transitional or mixed ratios in convexity from west to east. Thus shell globosity generally increases with depth.

Shaly, offshore facies also generally show a size decrease in atrypids, with the largest shells occurring in shallower carbonate facies on Gotland. This is the opposite to the suggestion of Fürsich and Hurst (1974) that the Wenlock Limestone specimens of '*Atrypa reticularis*' (probably *Atrypa affinis*) increased in size with deepening facies. They speculated that this was the result of a 'highly efficient lophophore' and 'less available' food. No evidence was found to support this concept, as all *Atrypa* have numerous whorls, and food availability is not possible to evaluate. No data are available on abundance of bacterial or phytoplankton, nor nutrients in these settings. There was no general stratigraphic correlation for size in *Atrypa*, i.e., increasing or decreasing size varied with time through the Wenlock and Ludlow. Large and small species occurred at random stratigraphically, more likely in tandem with environmental selection of species. One exception may be that for *Atrypa sowerbyi*, a large species from the eastern Hemse, biostromal, proximal facies, and *Atrypa munchisoni*, a small species from the deeper, distal Hemse facies to the west. This suggests that some larger species may have preferred shallower facies.

Internal variation in *Atrypa* is more difficult to verify as it relies on large collections with the internal views of valves available, or large numbers of serial sections from different specimens (because of the amount of time required for sectioning, i.e., 2–3 days per specimen, the latter is not normally practical). In serial sectioning multiple specimens from a population, the nature of the spiralia, jugal processes,

crura, pedicle callist, and teeth (dental cavities, orientation, size) was found to be consistent within species. For *Oglupes muldea*, considerable variation in the muscle patterns was also determinable within populations: the incision of the muscle scars, location, and shape of vascular canals, and impression of gonadal pits appear to be highly variable within the species (see figures). These are thereby discounted as specific characters, suggesting also that internal moulds are not reliable species indicators. Bowen (1966) noted similar variation in the nature of the dorsal cardinalia of a species of Early Devonian *Atrypa* from New York, but suggested environmental variation in this character with sediment type related to energy conditions, instead of intrapopulation variation. Thus it appears that general characters, such as the nature of the teeth and sockets, crura, and lophophore supports are relatively consistent within species, and show evolution with time, thereby useful for species distinction.

On Gotland, five species or varieties of *Atrypa* have been previously described, or cited in the literature. These include *Atrypa (Atrypa) reticularis* (Linnaeus, 1758), *Atrypa (Atrypa) alata* Hisinger 1831, and '*Atrypa reticularis* var. *concentrica*' (Munthe, Hede, and Lundqvist 1927, p. 21). The status of *concentrica* from the Höglint beds is unclear, as no type specimen, nor description, nor illustration exists. Schmidt (1858, p. 210) cited a '*Spirigerina undifera* n. sp.' from the Baltic Basin, which 'schliesst sich eng an *S. reticularis* und *imbricata*' [transl. = which is closely related to . . .], but this species appears to have become a nomen nudum, as no figures have ever been published, and a type specimen is also unknown. Rubel (personal communication) suggested that the localities cited for *undifera* indicate a species from the Porkuni beds of Ashgill age, and are unlikely to be *Atrypa*. Lindström (1885, p. 12) also cited '*Atrypa* var. *squamosa* Lovén in Museo', but neither type nor description exists for this species either, and it is not certain if this refers to *Atrypa*.

Species and subspecies assigned to the subgenus Atrypa (list incomplete).

Terebratulina affinis Sowerby 1822, probably Dudley, Britain, Much Wenlock Limestone, late Wenlock.

Atrypa reticularis var. *alata* Hisinger 1831, Näskyrka, Gotland, lower Eke beds, Ludlow.

Atrypa lazutkini hatschatensis Rzhonsnitskaya 1975, Gurev, Kuznetsk Basin, Chernobobachat beds, late Lochkovian.

Atrypa chulutensis Rozman 1988, Gobi Altai, Tsaganbulak beds, late Wenlock.

Atrypa reticularis var. *dzwinogradensis* Kozłowski 1929, Dzwiniogorod, Dzwiniogorod beds, Podolia, Ukraine, late Ludlow.

Atrypa (Atrypa) gotha n. sp., Gotland, Upper Visby beds, early Wenlock [see below].

Atrypa fumosa Havlíček 1991, Kozolupy, Czech Republic, lower Kopanina Fm., early Ludlow.

Atrypa reticularis var. *harknessi* Alexander 1949, Bradlow, Britain, Wenlock Shale, early–middle Wenlock.

Atrypa krekovskensis Rzhonsnitskaya 1968, Gurev quarry, Kuznetsk, upper Krekov beds, late Pragian.

Atrypa reticularis kuzbassica Rzhonsnitskaya 1960 [replaced by *A. markovskii*].

- Atrypa reticularis* var. *lapworthi* Alexander 1949, Nacklestone, Wenlock Limestone, late Wenlock – early Ludlow?
- Atrypa lazutkini* Alekseeva 1960a, Gurev area, Tolstochikh hill, Tomchumysk Horizon, Lochkovian.
- Atrypa* (*Gotatrypa*) *lindstroemi* Struve 1966, Gotland, Hemse beds, Ludlow [= *A. sowerbyi*].
- Atrypa losvensis* Mizens 1977, E slopes N Urals, Striatov Horizon, Ludlow.
- Atrypa margarita* Barrande 1879, east of Litice, Czech Republic, Motol Fm., Wenlock.
- Atrypa reticularis* var. *murchisoni* Alexander 1949, Ledbury, Britain, lower Ludlow Shales, Ludlow.
- ?*Terebratula reticularis* var. *murchisoniana* Barrande 1847, Prague Basin, Ludlow.
- Atrypa markovskii* Rzhonsnitskaya 1968, Tom-Chumysh River, Kuznetsk, Salair Horizon, middle Emsian.
- ?*Atrypa nagorskii* Khalifin 1948, Altai Mountains, Lower Devonian.
- Atrypa oklahomensis* Amsden 1958a, Fittstown, Oklahoma, Haragan Fm., Lochkovian.
- Atrypa plana* Sowerby 1839, Tynewidd, Wales, Wenlock.
- Atrypa* (*Atrypa*) *slitea* n. sp., Gotland, Slite beds, Wenlock [see below].
- Atrypa reticularis* var. *sedgwicki* Alexander 1949, Malverns, Britain, Aymestry Limestone, Ludlow [= *A. reticularis*].
- Atrypa reticularis* var. *sowerbyi* Alexander 1949, Sedgley, Britain, Sedgley Limestone, Ludlow.
- Atrypa tennesseensis* Amsden 1949, Blue Mound Glade, Tennessee, '30–45 ft. above base Brownsport Fm.' (1 ft. = 0.305 m), Ludlow.
- Atrypa torquata* Havlíček 1991, Dlouha Hora, Czech Republic, upper Kopanina Fm., late Ludlow.
- ?*Atrypa transversa* Khalifin 1948, Altai Mountains, Early Devonian.
- Atrypa reticularis* var. *woodwardi* Alexander 1949, Dinchope, Britain, *Dayia navicula* beds, middle Ludlow.

Atrypa (*Atrypa*) *reticularis* Linnaeus, 1758

Pl. 2, figs. a–o; Fig. 12

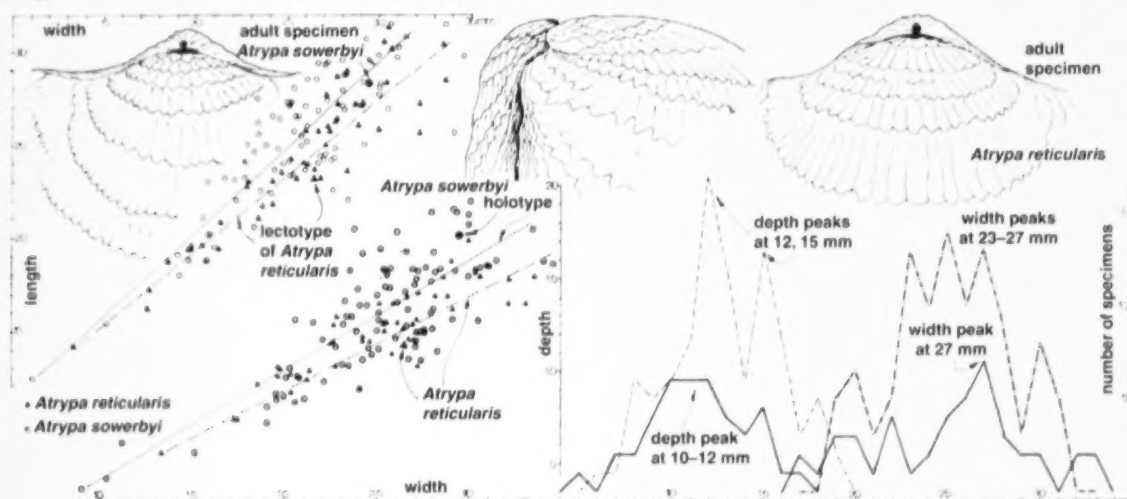
- 1758 *Anomia reticularis* Linnaeus, p. 702 [Davidson, 1866, p. 4, dated this species as being printed in the second volume of *Systema Naturae* in 1767, but most others accept 1758].
- ?1828 *Atrypa reticularis*, Dalman, p. 127–128, pl. 4, figs. 2a–c.
- ?1829 *Terebratula cancellata* Eichwald, p. 276, pl. 4, fig. 11 [glacial alluvium from Vilnius].
- 1949 *Atrypa reticularis*, Alexander, pl. 9, figs. 1a–d [lectotype selected].
- 1949 *Atrypa reticularis* var. *sedgwicki* Alexander, p. 215–216, pl. 10, figs. 5a–d.
- 1967 *Atrypa reticularis*, Brunton, Cocks, and Dance, p. 170–171, pl. 2, figs. 19–23 [lectotype figured].

Type locality: 'In Gottlandiae calce' (Dalman, 1828, p. 127). In 1758 Linnaeus did not illustrate any specimens, nor indicate a collecting locality. Despite the widespread reports and illustrations of this catchall species from many parts of northwestern Europe, the only illustrations of *Atrypa reticu-*

laris [sensu stricto] occur in Alexander (1949), Copper (1965), and Brunton et al. (1967). The exact type locality is not identified by Linnaeus in his description, nor known from labels in the Linnean Society, London, type collection [examined in 1963]. Neither were Hisinger (1827, 1831b, 1837) and Dalman (1828) specific about their exact Gotland location for specimens, although this may well have been a collecting locality popular at the time. Murchison (1847) cited '*Terebratula reticularis*' as coming from 'Grötlingbo' [map sheet 5J Hemse NV — about 11 km S of Hemse, where the upper Hemse and Eke beds crop out]. He extended the species through all the strata on Gotland: this specimen is possibly *Atrypa sowerbyi* (Alexander, 1949) from units D–E of the Hemse Formation, but Murchison was close to the type horizon, if that is so. The type Linnean collection contains a number of specimens, only two of which can be assigned to *reticularis* sensu stricto (Brunton et al., 1967). Linnaeus probably acquired his lectotype specimen of *reticularis* from easterly shoreline outcrops at or near Hammararen (Östergarn parish), or an adjacent site in the lower Hemse beds, since these are the only exposed strata on Gotland which have yielded material identical to the lectotype [see below]. The coastal localities were probably more accessible, as they provided a number of other early type species (e.g., *Didymothyris didyma* from almost the same level of the Hemse beds as *Atrypa reticularis*). Some have indicated the Mulde Marl brick quarry as the possible type locality, but there are no specimens in the Linnean collection which match the brickyard species *Oglupes muldea*, and no true *Atrypa* have been found there by me in either new or older collections.

The locus typicus restrictus is here defined as **Hammarudden 3** [Östergarn parish, 6J Roma SO 73170:84550; this may be equal to 'Hammarudden' of 19th century collections; refer also to Munthe et al., 1929, p. 31, Färsviken locality]. This is a shoreline bedding plane outcrop, exposing, partly underneath seaweed, about 50 cm – 1 m of thinly bedded, hard, somewhat nodular grey micrites with shaly partings containing rare to common *reticularis* associated with small favositids, rare syringoporids, and common gastropods. The original locality yielding *reticularis* may have been exposed anywhere along the shoreline for a distance of some 600 m between **Hammararen 1** and **Färsviken 1**. Old collections from the Riksmuseet, Stockholm, labeled '**Hammarudden**' are most like the type specimen, and include one or two specimens virtually identical to it. Schmidt (1859) shows localities called 'Hammarudd', NE of Kräklingbo, and 'Katt-hammarsvik' on the east coast, which appear to have been known as fossil localities in the first century after Linnaeus. Jaanusson (personal communication) believed that the older collections of *reticularis* dating from the last century must have come from Östergarn parish, which includes these beach localities, and my data agree with this. On modern maps [6J ROMA NV NO], 'Hammarudden' is the southernmost coastal point on the map, but careful searching of the coastline has thus far failed to reveal layers rich in *Atrypa*; although strata near here contain isolated specimens. There are two localities called Hammarudden, placed on the Munthe et al. (1929) geological map, both in Hemse strata. The first, the 'Hammarudden' type coastline locality (Östergarn parish), is located about 3–4 km NNE of Östergarn church,

Fig. 12. *Atrypa (Atrypa) reticularis* Linnaeus, 1758. Statistical comparison of *Atrypa reticularis* (Linnaeus, 1758; solid line) and *Atrypa sowerbyi* Alexander, 1949 [broken line] based on compilation of data from both species; width/length and width/depth curves reflect morphology. Camera lucida sketches of *A. sowerbyi* (upper left) and *A. reticularis* (both upper right), Hemse beds, Ludlow.



and has produced specimens here assigned to *A. reticularis* s.s. The second Hammarudden locality is located in Kräklingbo parish. Schmidt (1859) described this locality by stating, 'at Hammarudd point we saw a stromatoporoid and syringoporoid limestone intercalated by dark grey marls . . . overfilled with *Rhynchonella diodonta* . . .' [free translation]. Jaanusson (1986, p. 14) identified this locality as Garnudden 1: abundant rhynchonellids, but no *reticularis*, occur here in thin shaly layers between thinly bedded limestones. There are numerous, intermittently exposed localities in salt marshes south along the shoreline from locality Garnudden 10, south of Hammarudden, and past Djauviksudden, many with domed stromatoporoids, platy favositids and heliolitids with small brachiopods. I was unable to find any *Atrypa* in shoreline localities explored for a distance of 3 km south of Garnudden, past Djauviksudden. This would seem to exclude the second 'Hammarudden' as a possibility for the source of *A. reticularis*. The coastline may have changed considerably in the last 200 years since the Linnaeus specimens were collected, and winter storms could have removed or added sediments, and seaweed may have obscured the original outcrop.

Type stratum. The Hemse Formation, unit C on the east coast [sensu Hede, 1960] is named here as the stratum typicum. Lars Ramsköld (personal communication) has identified an encrinurid cranidium, which is fixed to the lectotype specimen of Linnaeus, as *Bolizoma obtusum*, which is said to indicate strata of Hemse 'C' age. This has been placed by Laufeld and Jeppsson (1976) within the *Monograptus scanicus* Zone, i.e., middle Gorstian, early Ludlovian. The strata containing *reticularis* lie directly below a shaly unit with a rich fauna of relatively large *Didymothyris didyma* [this is undoubtedly the type locality of *didyma*], and *Protochonetes* at Färsviken 2 [72780:84750]. It is notable that no *Dayia* occur within these Hemse strata (units A–C) in NE Gotland. Alexander (1949) remarked that she believed that the type species of *Atrypa* came from the 'Mulde Märgelstein', but

the abundant species from the upper Wenlock Mulde shales is *Oglupes muldea*, which is very different, and easily distinguished from *Atrypa reticularis*. Brunton et al. (1967) were uncertain about the source strata of *reticularis*. The only somewhat similar specimens from Britain (cf. *A. reticularis sedgwicki* Alexander 1949) come from the Aymestry Limestone (late Gorstian) of slightly younger Ludlow age than *A. reticularis* [s.s.]. The Aymestry Limestone of the Malverns is usually placed within the *tumescens* Zone, and younger than *reticularis* on Gotland. Therefore, it is probable that *A. reticularis* ranges from the *scanicus* Zone into the *tumescens* Zone, where it overlaps with *Atrypa sowerbyi*.

Diagnosis. Relatively large, shield-shaped *Atrypa*, nearly as wide as long, peak 23–27 mm wide, ca. 5–7 ribs per 5 mm, growth lamellae spaced at rhythmic 2–3 mm intervals; gently rounded, weak anterior fold.

Description. Large shells (maximum 38 mm wide, averaging 27 mm), depths averaging 10–12 mm; broad, relatively straight hinge with 140°–160° hinge angle; moderately indented shoulder line; beak protruding slightly; ventral umbo weakly inflated, rest of vv relatively flat to weakly concave; moderately to strongly convex dv, broadly rounded, rarely highly arched; ribs relatively fine at 6–7 per 5 mm, nearly tubular in aspect, and only weakly curved to wavy at growth interruptions; ribs expanding slightly at each growth lamella; growth lamellae, regular, rhythmic at earlier stages, but crowded, overlapping at commissure; lamellae weakly deflected in early stages but may be strongly deflected in maturity to senility; frills up to 5–7 mm long; lamellae may be slightly prolonged in troughs over crests giving scalloped appearance to breaking edges; foramen obscured by hypercline-adpressed area, or commonly transapical in adult stages; early growth stages with weakly anacline area, small apical foramen, small deltidial plates visible in well-preserved neanic specimens; weakly folded to almost rectimarginate commissure.

Ventral valve with weak to modest pedicle callist, rarely collar; small dental nuclei; distal portions of teeth rarely with small dental cavities; dorsomedially to dorsally directed teeth short, thick, wide, massive, with short lateral lobes; ventral diductors scars rounded, variably large, from 1/3 to 1/2 shell length; vascular canals clearly visible as anteriorly tapering ridges, bifurcating towards commissure; gonadal pits strongest around diductor margins. Dorsal valve with strong cardinalia; cardinal pit and inner socket ridge lined by short, small cardinal process; crura, jugal processes, spiralia not preserved in sectioned specimen.

Remarks. Alexander (1949), in her revision of the type species from Gotland and identifying other species of *Atrypa* from England and Wales, selected as lectotype a specimen from the Linnaeus collection (Royal Society, London): this is re-illustrated here [from my 1963 photographs of the type]. This specimen is identical to material from Hammarudden 3, the type locality. The illustration provided by Dalman (1828), shows a somewhat more coarsely ribbed [5–6 ribs per 5 mm] variety of *Atrypa*, possibly not *reticularis*, about 26 mm wide (but matching the dimensions of the Linnaeus type). Dalman cited no collecting locality for his illustration, and mentioned in his description that the shell was about 35 mm wide (perhaps including the frill seen on some specimens), and had 40–60 growth lamellae, and about 20 ribs per shell.

The species most similar to *A. reticularis* is *A. sowerbyi* Alexander 1949 [= *A. lindstroemi* Struve, 1966; see following description]. *A. reticularis* distinguishes itself in having a longer, straighter hinge line, a flatter, shield shape, higher width/length and width/depth ratio, and in generally being larger in size, and more coarsely ribbed than *A. sowerbyi*. *A. sowerbyi* is also more elongated, narrower, smaller and has a rounded to ovate outline. The poorly preserved specimen described by Alexander (1949) under the subspecies name *sedgwicki* ['Aymestry Limestone' at Norton Camp near Craven Arms, Shropshire, but probably lower than that stratigraphically] is here regarded as a junior synonym of *A. reticularis*. If the age of the Gotland material is correct, this limestone at Norton Camp is as young as the *scanicus* Zone. Further material from this, and nearby localities, in the Alexander collections or elsewhere, is listed. The British species *A. sowerbyi* is most similar to a locally abundant Gotland species occurring 20–30 m higher in the upper Hemse beds (units D–E) on Gotland, and is of *tumescens-leintwardinensis* age. These identifications suggest that the age of the Hemse beds on the NE coast ranges from the higher *nilssoni* through lower *leintwardinensis* zones, and on the SE coast down as low as the basal *nilssoni* Zone.

Materials. 114 specimens: this subspecies appears to have a restricted distribution confined to the marginal marine platform of the east coast of Gotland, and Hemse 'C' units, from the *scanicus* Zone. **Hammarudden 3** [restricted type locality], shoreline outcrop, thinly bedded micrites, bedding plane surfaces with syringoporids, favositids, 6J Roma SO 73170:84550 [SW93: 7; SW70: 1]; **Hammarudden 1**, Br104655 [1], Br104051-1 [2], Br115444-61 [18], Br115462-88 [27], Br122596-99 [4], Br43587 [1]; **Färsviken 1**, light grey thinly bedded micrites with syringoporids, 6J Roma SO 72720:84720 [SW91: 2]. **Hammarudden 2** is the probable

type locality of *Didymothyris didyma*, a very abundant, bed-forming athyridid species there. In Britain *A. reticularis*, identified as '*Atrypa reticularis sedgwicki*' by Alexander (1949), is true *reticularis reticularis*, and allegedly comes from the 'Aymestry Limestone' (probably lower parts, or more likely, below the Aymestry Lst. sensu stricto) at the following locations in Herefordshire: **Norton Camp**, type locality near Craven Arms, A11625 [holotype *A. sedgwicki*], A30473-81 [9]; **Cop Hall Hollow**, quarry on E side, 3/4 mile (1 mile = 1.61 km) N of Downton, A56710-4 [5]; **Rottingwood** quarry, 150 yds. (1 yd. = 91.4 cm) S of Rotting Lane where it enters the wood, Norton Camp, A56700-1 [2], A56781-4 [4]; **Norton**, N of Rottingwood, A56702-5 [4]; **Whettleton Wood**, in path 500 yds. N of Norton Camp, A56698-9 [2]; **Dinchope**, Shawbank quarry, A56718-9 [2]; **Dinchope 109**, A30472 [1]; **Brandhill 13**, 1/4 mile NW Brandhill farm, A30489 [1]; **Clungunford**, 1 1/2 miles E, A56706-9 [4]; **View Edge Farm**, quarry at top escarpment, 5 furlongs SW farm, A56781-4 [4]; **View Edge**, A30486-7 [2]; **Whealers Vallets**, 3300 yds. ESE, Dingle crossing, A56715-7 [3]; **Aldon 10**, quarry in Springhead, A30490-2 [3]; **Springhead Gutter**, quarry at E end, A56675-6 [2], A30490-2 [3]; **Mocktree** Hayes, A30382-5 [4]; **Halford Wood**, centre of old quarry, A56785 [1], A30472 [1].

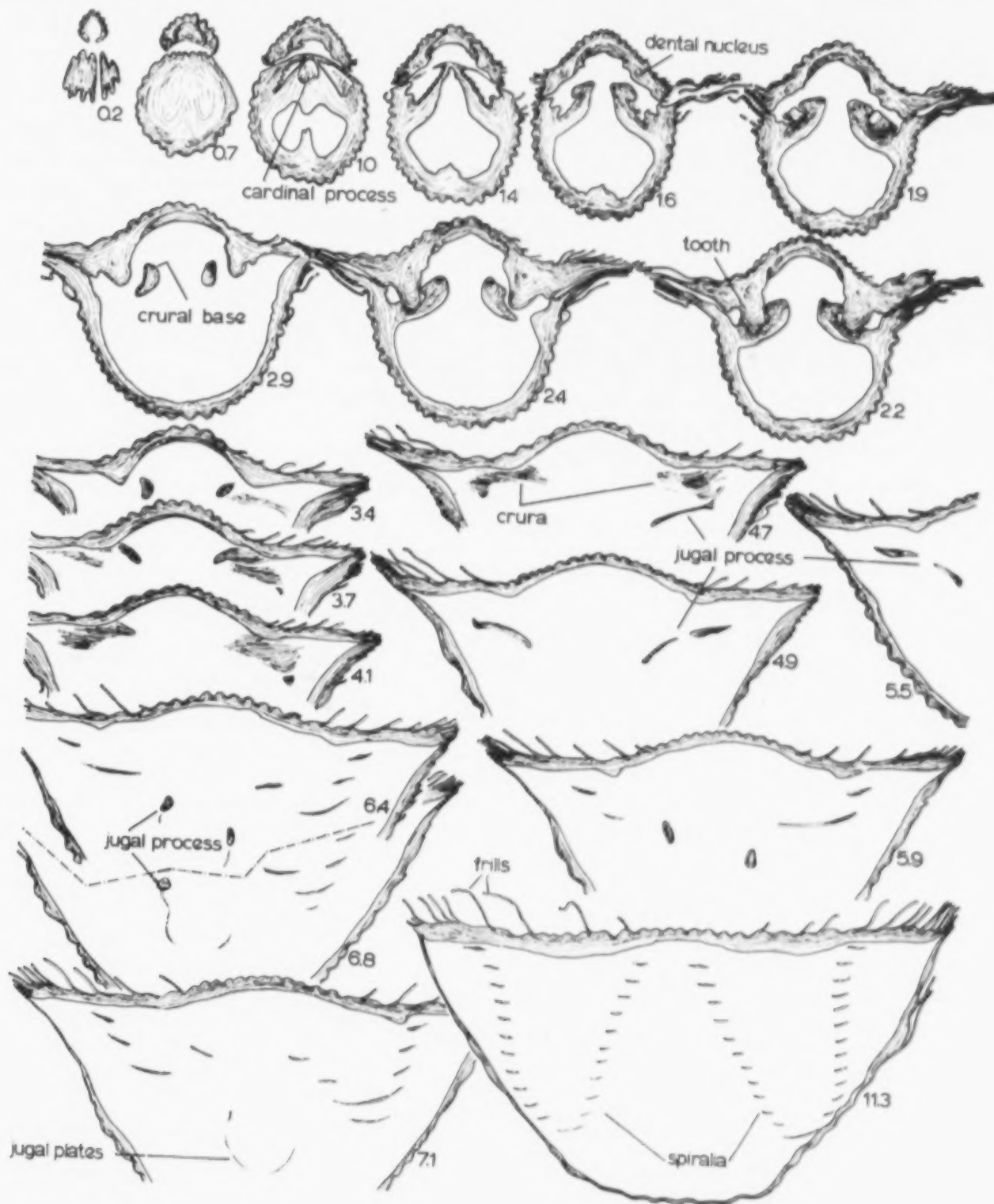
Atrypa (Atrypa) sowerbyi Alexander, 1949

Pl. 1B, figs. a–c; Pl. 3, figs. a–v; Figs. 12–14

- 1837 *Atrypa reticularis*, sensu Hisinger, pl. 21, figs. 11a–c [in the text, Hisinger specifically mentions the old Näs locality where the species occurs in the Hemse beds with *Dayia*, and size and shape illustrated are typical].
 1925 *Atrypa reticularis*, Munthe, Hede, and von Post, pl. 1, fig. j [specimen from upper Hemse beds, Burs].
 1949 *Atrypa reticularis* var. *sowerbyi* Alexander 1949, p. 216, pl. 9, figs. 2a–d [Shropshire specimens].
 1966 *Atrypa (Gotatrypa) lindstroemi* Struve, p. 133–134, pl. 15, figs. 7–9 [locality unknown].
 1967 *Atrypa reticularis*, Brunton, Cocks, and Dance, pl. 2, fig. 25 [Linnaeus colln., upper Hemse beds].
 1969 *Atrypa reticularis*, Harper, figs. 1, 4 (only).

Type locality and stratum. 'Sedgley, Staffordshire' (Alexander, 1949, p. 216). Little additional material (only 12 specimens) was available from this or other localities in the Natural History Museum or Sedgwick Museum collections. The type stratum is the Sedgley Limestone of south Staffordshire (Alexander, 1949; called the 'Aymestry Limestone' of Sedgley), within the lower-middle *leintwardinensis* Zone, Leintwardinian, middle Ludlow, said to be equivalent to the Eke beds of Gotland. In Gotland, this species is present in the upper Hemse beds, upper part of units D–E, over a region of central Gotland extending from west of Hemse to the northeast coast. The facies changes to higher energy and shallower waters in the Eke beds, where *Atrypa* is absent, being replaced by the genus *Andrea*. Laufeld and Jeppsson (1976) proposed that these higher Hemse units range from the middle *scanicus* through lower *tumescens-leintwardinensis* zones: the atrypids suggest that most of units D and E in which the species was collected is of *tumescens* to *leintwardinensis* age. These strata are thinly bedded, soft-weather-

Fig. 13. *Atrypa (Atrypa) sowerbyi* Alexander, 1949. Serial sections of Br104047, Grogarnshuvud I, Hemse beds, Ludlow; note the very long jugal plates extending dorsally, bushy crura, small cardinal process in cardinal pit; $\times 4$.



ing micrites to calcarenites with many whole as well as broken shells, bearing *Atrypa* frills on bedding plane surfaces. This species has a much wider distribution than *A. reticularis* s.s., being found in central to western proximal shelf facies as well as the shoal to peri-reefal areas. A commonly co-occurring small species of *Davia* is common, and usually more abundant, especially in the western outcrops, and *Atrypodea primum* is found associated in some of the northeastern outcrops.

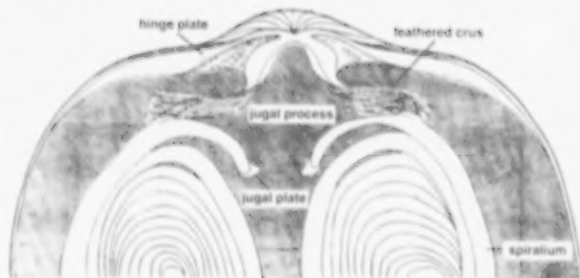
Diagnosis. Ovate, dorsibiconvex to partly convexoplane *Atrypa*, averaging 25 mm wide, as wide as long, peak 12 mm deep, 8–10 ribs per 5 mm, highly rhythmic, 1–3 mm spaced growth lamellae, and usually with only the last, wide frill extended beyond the shell (where preserved).

Description. Medium-sized to large ovate shells, ranging from 23 to 27 mm width (maximum 31 mm), moderately deep shell (peaks 12–15 mm); outline usually well rounded, less commonly shield-shaped; vv nearly flat to weakly resupinate; hinge line weakly indented; anterior dorsal fold weak or moderate, gently curved; ventral beak small, barely protruding, adpressed; foramen transapical, minute, <1 mm; neanic shells (<5 mm wide) demonstrate an orthocline area, apical foramen, minute deltidial plates. Ribs fine, consistently spaced at 8–10 per 5 mm, most commonly bifurcating on vv (invariably at the beginning of a new growth lamella, on adult frills ribs intercalated on frill surface); growth lamellae produced in wave-like undulations, systematically spaced on individual shells at 1–3 mm, edges commonly breaking regularly, less commonly ragged; growth lamellae crowded on anterior margin of adult shells, overlapping, frills long, up to 5–8 mm, closely hugging dorsal valve surface, then projecting concentrically; on vv projected at sharper angles to shell surface; frills normally detached during life, with usually only final frill forming single flange around shell; worn frills becoming round-cornered at hinge, with wide frills somewhat more rectimarginate posteriorly; at breaking point growth lamellae commonly, but not invariably, with elongate, postage stamp-like perforations, marking breaking edge of frills.

Shell relatively thin walled, vv with thin to moderate pedicle callist, collar protruding into foramen; short, stubby teeth with small dental nuclei, in early growth stages (<5 mm width) with small dental cavities, very short lateral lobes, dorsally directed; round, large diductor scars, one third to half shell length, weakly impressed with raised rims, weakly striated; adductors small, central, faint; vascular canals faint, branching laterally; gonad impressions distinct, shallow. Dorsal valve with weak cardinal process in cardinal pit; hinge plates relatively thin; inner socket ridges bulbous, expanding into small crural bases; crura curved laterally into bushy crural fibres; widely spaced jugal processes terminating in very long, slender, slightly curved, jugal plates reaching deep into dv; adult spiralia ca. 12 whorls, D-shaped at base of spirillum.

Remarks. One of the remarkable features seen in rare shells is the row of perforations at the frill junction with the shell surface; this must have enhanced the ability of the shell to detach its wide frill periodically during growth. The shell retained only the last, or last several frills produced. This dou-

Fig. 14. *Atrypa (Atrypa) sowerbyi* Alexander, 1949. Reconstruction from serial sections, Br104047 Grogarnshuvud 1, Hemse beds, Ludlow; approx. $\times 3$.



ble feature of a thin frill and perforations could well account for the very great scarcity of preserved frills in this species, as frill shedding during life must have been common. Both the ventral valve and brachial valve commonly retained one frill, or sometimes several wide, overlapping frills at the shell margin. The ventral valve frills also served to raise the shell above the substrate. This species is distinct from the slightly older *A. reticularis* s.s. from lower Hemse strata in being finer ribbed, equidimensional to elongate (versus wider than long), somewhat smaller, with a more highly arched dv (see *Atrypa reticularis* statistics). It is more widespread and abundant in the Hemse beds than its predecessor, being found on the western side and in the central facies of the Hemse, as well as the east side. From other species of *Atrypa* in NW Europe, it differs in its very distinctive and regular growth lamellae and fine ribs.

Struve (1966) reported that the holotype of *Atrypa lindstroemi* (a junior synonym) was collected at 'Kräklingbo-Hammar' from the 'Klinteberg beds'; it is highly unlikely that the species came from the Klinteberg Formation (from which only *Atrypa affinis* is known, and not a single specimen of *A. reticularis* or *sowerbyi* was available or collected). The shell illustrated by Struve (1966) is identical in terms of its fine ribs and evenly spaced growth lamellae to specimens from Hemse D–E levels, and synonymous with the Alexander species *A. sowerbyi*. Harper (1969) attempted to analyse the rib insertion pattern of *A. sowerbyi* (which he called *reticularis*) from the upper Hemse beds in the same strategy attempted by Kelus (1939) and Struve (1966) for Atrypidae. Initially this was also carried out for several hundred shells of Gotland and British Atrypida, but no specific insertion scheme was predictable, as ribs were intercalated or bifurcated in apparently random patterns on both valves, so as to maintain rib spacing at constant densities.

Materials. Total 241 specimens, a very widespread subspecies in the middle to upper Hemse beds from the east coast to central Gotland near the village of Hemse. Specimens from Britain derive mostly from the 'Aymestry Limestone' (higher parts?). The type comes from the Sedgley Limestone at Sedgley, locality, A11626 [holotype], A30463–71 [9], A30493 [1], A59176–81 [6]; **Vue Hill**, A37415 [21]; **Leintwardine**, A37416–8 [3]; **Whitcliffe Wood**, A37419–21 [3]; **Downton 55**, 'quarry in field 1/2 mile SSW Downton', A30488 [1].

Gotland material. **Grogarnshuvud 1**, Br104028-48 [20: the locality is cited in Munthe, Hede, and Lundqvist (1929, p. 31)]; **Fie 1**, När sn., Br104653 [1]; **Linde 1**, Linde Klint, ostra sidan, Br46900 [1]; **Hammarns**, Br43380 [1]; **Laukanal**, nära bron, Br107967 [1]; **Laukanal**, Lau sn., Br108088-9 [2], Br124633 [1 vv], Br43284-6 [3]; Br43290-96 [7]; Br43305-7 [3]; Br43297-304 [8]; SSO am bron, Br124728-38 [11]; ca. 100 m NNV am bron, Br124634-5 [2]; **Ronekanal**, Burs sn., vid Vesterlaus, no Br [2]; **Burs sn.**, Br108046 [1]; **Grogarns 4**, shoreline outcrops S of Grogarnshuvud, with common *Atrypoida prunum* [SW21, 17]; **Grogarns 5**, about 150 m S of SW21, shoreline outcrops exposed at low tide [SW22: 2]; **Hemse 1**, sewer excavation in Hemse, south outskirts, 5J Hemse NV, NW of Kodings 1 [SW27: 24]; **Kodings 2**, ditch excavation, 5J Hemse NV [SW28: 32]; **Sigvalde 2**, reefal limestones near Sigvalde 1, Etelhem sn. [SW33: 2]; **Bengts 1** [Bents on old maps of Munthe et al. 1929], north side of road cut about 1 km directly E of Östergarn, along road to Herrvik west central Gotland, 6J Roma SO, Br106572 [SW26: 3]; **Gannes 4**, ditch outcrop alongside road, 1 km NW Östergarn, with abundant *Atrypoida prunum* [SW90: 1]; **Lilla Rone**, storanskanal, Lye sn. Br43495 [1], storan vid Lilla Rone, Br43910-11 [2]; **Östergarn**, Br43033-34 [2]; Br122600-5 [6]; Br43020-32 [13]; **Hulte 1**, Hemse sn., Br124632 [1]; **Hulte 3**, Hemse sn., Br129354-7 [4]; Br124629-31 [3]; **Grogarnsberget**, öst sidan, Br43424-9 [5 + 8 spec. without number]; **Mästermyrkanal mellan**, nullan diken, Sproge sn., Br? [1]; **Torsburgen**, Kräklingbo sn., Br43503-6 [5, two on one slab], Br124741 [1]; **Bomunds**, Burgen När sn., Br43226 [1]; **Tänaglins fiskeläget**, vid Englands hus, Etelhem sn., Br43393-4 [2]; **Fiskelagat Laubackar**, Br? [2]; **Lukse**, Hablingbo sn., Br124642-44 [3]; **Vanges Kanal**, Burs sn., Br43228-9 [2]; **Snausarve**, Lau sn., Br43281-2 [2]; **Tornklint**, Lojsta sn., Br43338 [slab with 4]; **Alva**, Alva sn., Br43224 [1].

Atrypa (Atrypa) gotha n. sp.

Pl. 4A, figs. a–f

Type locality and stratum. **Stavsklint**, ca. 300–400 m S of second 't' on name Stavsklint, highest point on Stavsklint cliff, Tofta skjutfält area, 6I Visby NO 39250-39350:83600-83850, uppermost Upper Visby beds, 3–5 m below Högklint resistant weathering cliff [access to cliff accompanied by Col. Lennart Ström]. This level is probably within the *murchisoni* Zone, early Sheinwoodian, early Wenlock. The species was found only in one other collection labeled 'Visby', but it is probable that it extends through the Högklint–Koparsvik beds into the lower Slite beds.

Diagnosis. Variable dorsibiconvex to nearly convexoplane shells; medium widths averaging 18–25 mm wide, depths 8–14 mm, as wide as long, very gentle anterior fold; relatively coarse, well-defined ribs, varying from almost flattened ribs to more strongly defined ribs; close, irregularly shaped growth lamellae.

Description. Medium-sized, rarely large, planate, biconvex – weakly dorsibiconvex young shells with rounded outline, adults convexoplane; vv only weakly convex to planar; dv more convex; maximum width near mid-shell length, widths 18–25 mm (maximum 35 mm), depths 8–14 mm (maximum

17 mm), as wide as long to slightly wider than long; hinge line straight to weakly indented; hinge corners subangular (adult) to subrounded (neanic); ribs ca. 6 per 5 mm, clearly defined at apex, shallowing to fading anteriorly, especially on growth lamellae; ventral mid-ribs enlarged, subcarinate apical 5 mm; growth lamellae irregular to regularly spaced, variable, at 2–3 mm; no wide frills observed. Shell internal details not available.

Remarks. The rare specimens precluded serial sectioning. This species, the oldest *Atrypa* (*Atrypa*) to appear in the Gotland succession, is distinctive in having growth lamellae that show planation of ribs to almost a loss of ribs, a relatively flat shell and wide hinge providing a shield-shaped outline to the shell. Its closest relative is *Atrypa slitea* n. sp., from the higher Slite Formation, which has very distinct and well-defined ribs, and shows no loss of rib definition on the growth lamellae. More material is required to carry out a statistical analysis. The species is overshadowed in the Upper Visby beds by its abundant counterpart *Oglupes visbyensis* n. sp., with a biconvex shell, wide frills, strongly defined ribs lacking planation.

Materials. Total 12 specimens. *Upper Visby beds:* **Stavsklint**, type locality, Br106589-91 [3 + 3]; **'Visby'**, Br110993 [1]. *Lowermost Slite beds.* **Ö. Vi. 1**, Visby sn., dike vid landsvägen till Endre Br103867-71 [5: some of these specimens grade into *Atrypa slitea* n. sp.].

Atrypa (Atrypa) slitea n. sp.

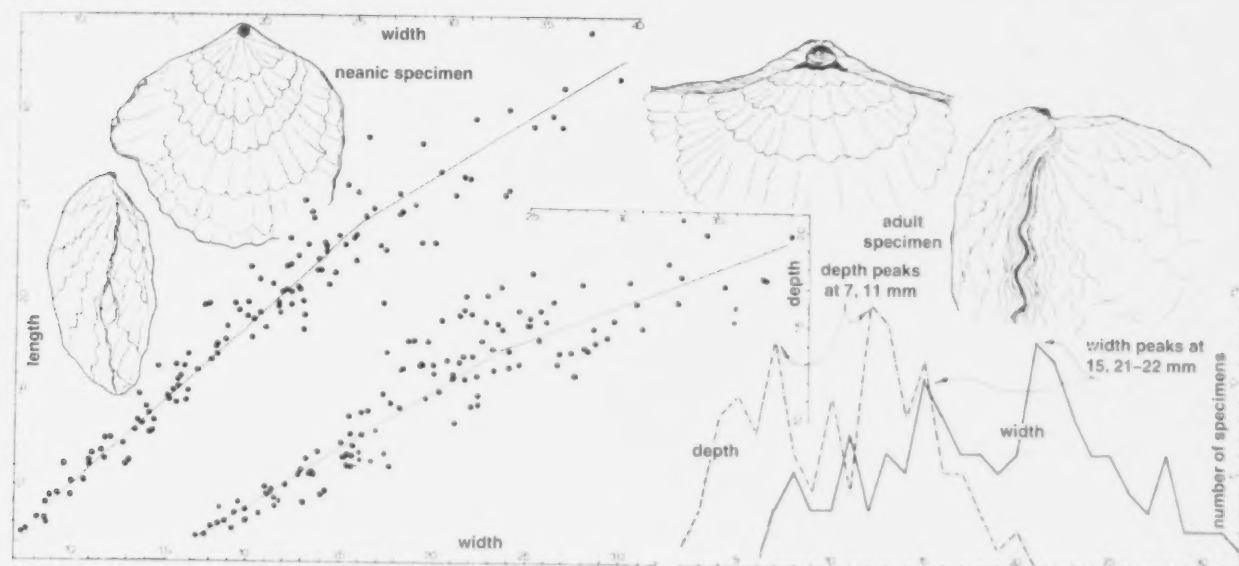
Pl. 5, figs. a–m; Figs. 15, 16

Type locality and stratum. **Hejdeby canal**, 500–700 m SSE of Hejdeby church (about 8 km due E of Visby); upper lower to middle part of the Slite beds. The species is quite widespread in northeastern Gotland in the softer, calcareous shale facies of the lower and middle Slite Formation, but it is rarely abundant at any one locality. The species appears to stretch from the middle *rigidus* Zone through middle *ellesae* Zone, i.e., middle to upper Sheinwoodian, with the holotype derived approximately from the *ellesae* Zone.

Diagnosis. Large *Atrypa* with wide, overlapping frills, making the ventral valve almost concave; 3–5 well-defined coarse ribs per 5 mm; ribs expanding in size on growth lamellae; shell shield-shaped with relatively straight hinge; anterior commissure defined by wide dorsal fold. Crura and jugal processes delicate; jugal processes terminating in gently curved jugal plates; spiralia with <15 whorls.

Description. Adult shells large (mostly due to distinctive, wide frill development), with adult peaks in width at about 21–22 mm, widest near hinge, about half as deep as wide, peaking at 7–11 mm; large shells showing growth change in width/length and width/depth ratios; outline shield-shaped to somewhat semicircular; long, nearly straight hinge, sharp hinge indentation adjacent to beak; ventral umbo adpressed, commonly perforated apically by foramen; prominent callist to small pedicle collar; vv weakly convex in early growth stages; rapid lateral growth by overlapping frills producing generally planate to marginally concave vv in adult shells; dv normally strongly convex in gerontic shells; anterior commissure with broad shallow fold; ribs coarse, 3–5 per 5 mm,

Fig. 15. *Atrypa (Atrypa) slitea* n. sp. Statistical variation of specimens compiled from all localities, Slite beds, Wenlock; camera lucida sketches of neanic and adult specimens.



somewhat shallow, occurring in waves shallowing at growth lamellar breakage points, coarsening anteriorly; growth lamellae spaced >3 mm, produced into 5–10 mm wide overlapping frills preserved at margins; frill-clear area left in central and umbonal portions with growth; breakage of frills irregular and ragged.

Pedicle cavity closed by distinctive thick pedicle callist, commonly funneled into collar; diductor muscle field large, incised by grooves and ridges anteriorly, moderately to weakly incised; central adductors not strong; dv with clearly defined, flabellate adductors, incised posteriorly by 3–5 grooves, separated by broad septum bifurcating around margins; sockets with middle socket ridges; small, bushy cardinal process wrapped around narrow, pinched cardinal pit. In serial sections, dental nucleus clear, sometimes expanded into small dental cavity; teeth relatively small to modestly sized, solid, dorsal in direction, with lateral lobes; dv socket plates thin, reinforced by hinge pad; middle socket ridges distinct; inner socket ridges small, flanking ventral teeth; crural bases small, delicate, expanding into fine crura, partly feathered, sharply deflected laterally; jugal processes with central nodular (?spinose) layer, terminating in very fine, straight jugal plates; spiralia with 14–15 whorls in adult shell.

Remarks. This species distinguishes itself in its relatively large size, planate to resupinate vv, coarse ribs, and straight hinge. It is most similar to *Atrypa alata* (Hisinger) from the Eke beds, but its straight hinge, clearly defined ribs, and widely spaced growth lamellae differentiate the two externally. Internally, the hinge plate and brachidia of *alata* are very wide and robust, whereas in *slitea* they are delicate. In the upper Slite Formation, this species is replaced by *Atrypa harknessi* Alexander, which is substantially smaller and more finely ribbed, lacking large frills. However, a species resembling *A. slitea*, but with somewhat finer ribs, and grading towards *Atrypa lapworthi* (Alexander, 1949), occurs in Hemse

facies in the Snoder area, stratigraphically below the Petesvik collections that contain *Atrypa muchisoni* (Alexander, 1949).

Materials. Total 127 specimens mostly from the central and eastern facies of the lower-middle Slite beds. This species is unknown from Britain. **Hejdeby canal** [type locality], 500–700 m SSE Hejdeby church, Br103373-88 [14]; dike vid **Suderbys**, Hejdeby sn., Br103441-3 [3], Br103447-8 [2], Br103452-9 [8]; dike 750 m N om **Martille**, Stenkumla sn., Br107893 [1], Br107897-909 [12]; **Österport**, dike vid landsvägen till Endre, ca. 150 m S Österport Visby, Br103861-2 [2]; **Storvede**, Br48849-58 [10]; **Slitebrottet 1**, SW entrance to quarry, in upper layers, 7J Färösund SO/NO [SW12: 70].

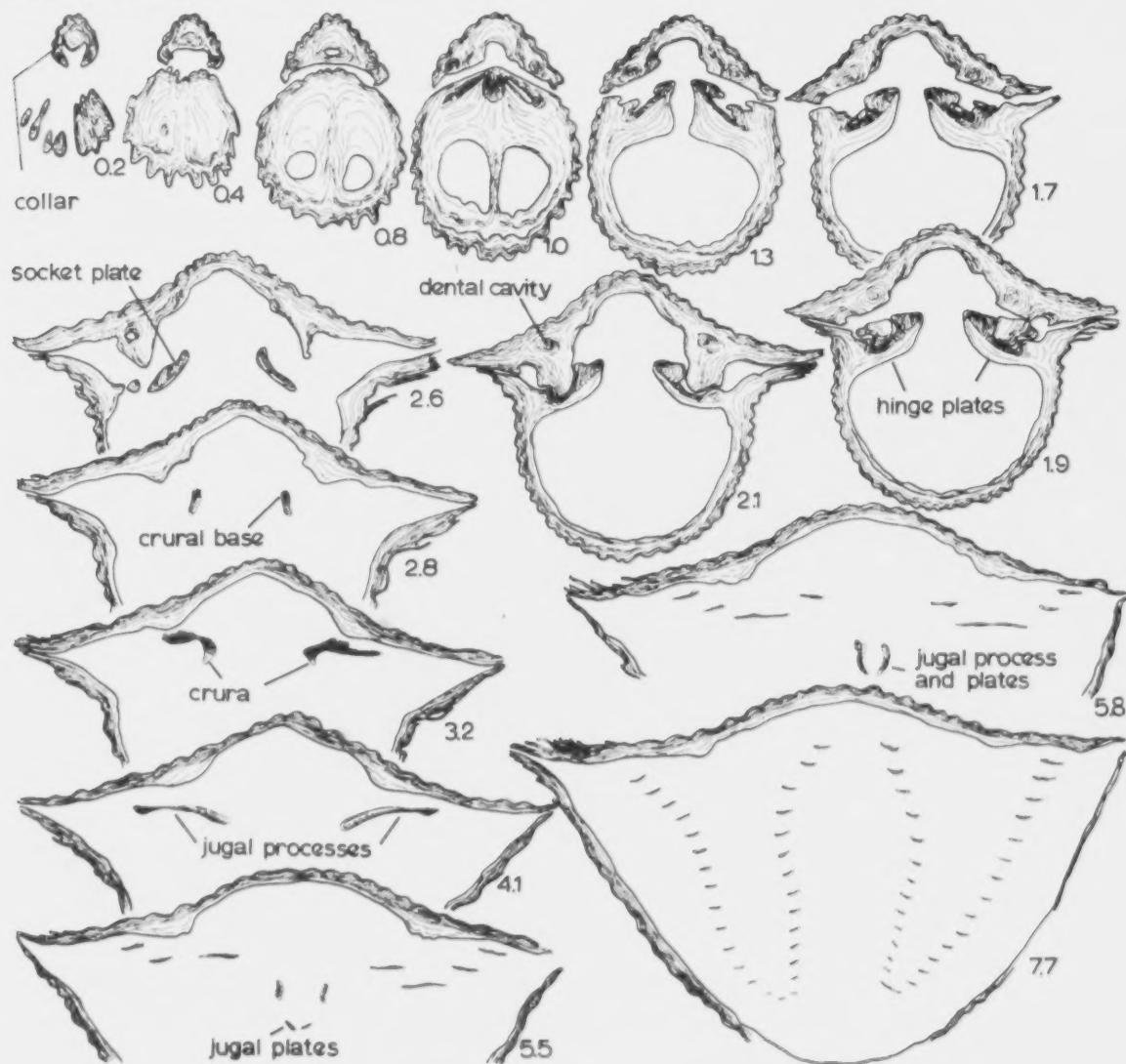
Atrypa (Atrypa) plana J. de C. Sowerby, 1839
Pl. 4B, figs. a, b

1839 *Atrypa plana* J. de C. Sowerby, p. 637, pl. 21, fig. 4.
?1852 *Atrypa reticularis*, G.B. Sowerby, pl. 11, fig. 203.

Type locality and stratum. 'Tynewidd, Llandovery' (Sowerby, 1839, p. 637). The lectotype, GSM661, one of four specimens on a slab selected by Cocks (1978, p. 156), is said to be from beds of Wenlock age [not to be confused with Llandovery age for the locality name near Llandovery], at Tynewidd, Dyfed, Wales; the exact Wenlock level is unknown, and the internal moulds themselves do not identify the nature of ribs or growth lamellae. Nearly all Wenlock and Ludlow *Atrypa* species have a relatively large ventral muscle field: e.g., Wenlock *A. slitea* and *A. harknessi*, Ludlow *A. reticularis*, *A. sowerbyi*, and *A. woodwardi* Alexander 1949, as seen in *A. plana*.

Remarks. There is inadequate material available for a clear diagnosis, and no complete shells. Sowerby (1839, p. 637) described the specimens, which can clearly be ascribed to *Atrypa* on the basis of flat shape of the vv and muscle scars,

Fig. 16. *Atrypa (Atrypa) slitea* n. sp. Serial sections of specimen from Slitebrottet 1, quarry entrance, Slite beds, Wenlock; note presence of pedicle collar, dental nucleus, jugal processes, and plates; $\times 4$.



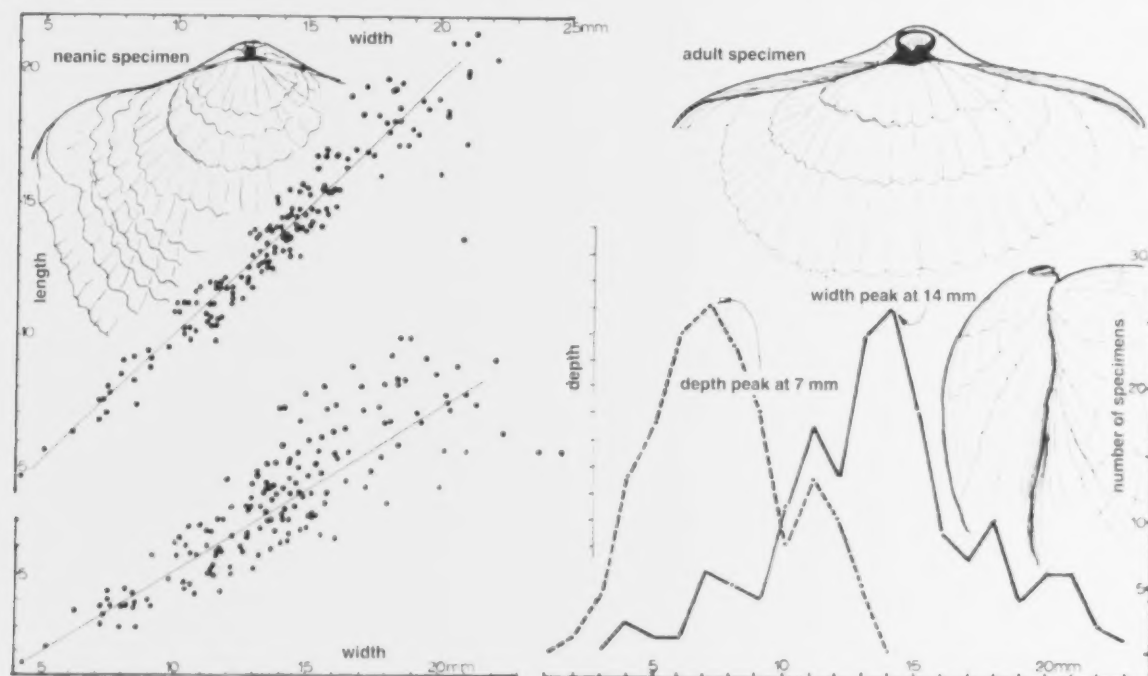
as 'orbicular, with the front rather produced, flattened, smooth . . . length about 7 lines, width 8 lines'. The width of 17 mm approaches that of a typical shell of *Atrypa harknessi* from the Wenlock Shale, which may thereby be a junior synonym, if size alone is helpful. Alexander (1949) made no mention of the Sowerby species from Wales. The lectotype selected from the upper left side of the slab by Cocks (1978) is clearly recognizable; the small slab contains the internal impressions of three other specimens, all loose valves in a dark brown sandstone matrix. No shell external structures, such as ribs or growth lamellae, are available, and this makes positive identification of this species uncertain with respect to others described. No internal shell material is available. A search for other specimens from this locality, or other similar material in collections in Britain, was unfruitful. The species is probably best regarded as a *nomen oblitum* or *nomen dubium* until new material is available from the type or nearby localities.

Atrypa (Atrypa) harknessi Alexander, 1949
Pl. 4C, figs. a–o; Fig. 17

1949 *Atrypa reticularis* var. *harknessi* Alexander, p. 213–214, pl. 10, figs. 2a–d.

Type locality and stratum. 'Wenlock Shale, Bradlow, near Ledbury, Herefordshire' (Alexander, 1949). Exactly where this species fits into regional stratigraphy is not clear. At Bradlow and near Ledbury, the Wenlock Shales, Wenlock Limestone, and lower Elton beds are all exposed. Penn and French (1971) identified three localities near Bradlow, one in Wenlock Limestone (no. 21), and two in Ludlow Shales (nos. 22 and 23). The collecting horizon of the various subspecies erected by Alexander was not investigated by Cocks (1978). I collected specimens assignable to *A. harknessi* at Whitman's Hill Coppice [W Malvern], along with speci-

Fig. 17. *Atrypa (Atrypa) harknessi* Alexander, 1949. Statistical variation compiled from localities at Bradlow, Malvern Tunnel, Whitman's Hill Coppice [Wenlock Shale, early-mid-Wenlock], and Hagsarve 6 (Gotland). Camera lucida sketches of immature and adult shell umbones.



mens similar to *Plectatrypa abbreviata* in levels probably fairly high in the Wenlock Shale. On Gotland, there are specimens similar to this form in strata near Klintehamn, ranging from the upper Slite beds to what Munthe, Hede, and Post (1927) mapped as shaly 'Hemse' beds directly above the Mulde Marl [but below the *Atrypa munchisoni* level around Petesvik]. The species is absent in the classical lower and middle Mulde Marl faunas that have *Oglupes muldea* n. sp. but is present in the Slite beds at the same locality where *Glossia djauvika* occurs in abundance. Another potential occurrence, although a slightly different form, is in localities around Hagsarve, in so-called 'Hemse' facies of the Klinteberg, i.e., in the high *ludensis* Zone on the SW side of Gotland. *A. harknessi* may thereby range from the higher *ellesae* through *ludensis* graptolite zones, i.e., spanning the Homeric or upper Wenlock.

Diagnosis. Small to medium-sized *Atrypa*, about 14 mm wide (average), with somewhat inflated umbo, usually short frills less than 5 mm long, a relatively narrow shell with ribs spaced at 5–7 per 5 mm.

Description. Medium sized, rounded to shield-shaped in outline, usually longer than wide; biconvex in early, convexo-plane in adult stages; average widths 14 mm, maximum width closer to hinge, depth peak 7 mm; hinge corners rounded; ventral umbo slightly inflated, projected above hinge; small transapical foramen; projecting pedicle collar; ribs weakly expressed, about 6 per 5 mm, tending to fade towards hinge corners; growth lamellae poorly developed, spaced at ca. 2 mm, overlapping at commissure; frills rarely developed, less than 5 mm long. No serial sections prepared.

Remarks. Alexander (1949) remarked that the species was somewhat similar to the coarser ribbed variety named *davidsoni* [assigned here to *Oglupes*]. However, new collections and re-examination of the old collections at Cambridge and the BMNH indicate that this judgment may have been superficial. The most similar shell is its probable descendant, *Atrypa (Atrypa) munchisoni*, which on average tends to be smaller and have almost a flat vv: the ventral umbo tends to be somewhat inflated in some *A. harknessi*. Typical forms resembling the British specimens occur in the upper part of the Slite Formation in the Klintehamn area (Klinte 7, 10). In addition, a slightly wider, larger variety of this shell occurs in the lowest part of the Hemse strata on the SW side of Gotland, around Snoder (Hagsarve 1, 2), stratigraphically below the lowest occurrence of *Atrypa munchisoni*, and above the Mulde Marl. This Snoder variety is possibly a new species; alternatively it could be a variant of *Atrypa affinis*, which possesses frills, although the ribs in *A. affinis* are differently developed.

Materials. Total 383 specimens. British specimens are from the Wenlock Shale (Coalbrookdale Fm. equivalents). On Gotland this species is present in the upper Slite beds, Mulde beds, and ranges to beds above the Mulde Marl, i.e., the western shaly facies of the lowermost Hemse beds. **Bradlow**, near Ledbury, A11621 [holotype], A56720–32 [paratypes–13], A30376–92 [paratypes–17]; **Malvern Tunnel** tip heap, Colwall Railway station, A30393–410 [17], A56733–42 [11], A56743 [27], A30311–6 [6]; **Whitman's Hill Coppice**, A4103 roadcut, GB13 [23]; **Wren's Nest**, east side Wenlock Shales, GB12 [68]. **Djupviksvägen 1**, upper Mulde Marl, 1.2 km WNW of Bopparve [SW44: 35]; **Sudervik 2**, coastal

outcrop of high Mulde shales, about 1.6 km S of Kronvalls fisklage [SW45: 2]; **Klinte 7**, E of intersection of Highways 140–41, ditch outcrops of upper Slite shales at south end of Klintehamn, Br106587-8 [SW95a: 53]; **Klinte 10**, ditches at intersection 140 and 141, S part of village, upper Slite beds [SW95: 58]; **Tjälldersholm 1**, outcrops exposed adjacent to small reefs at low tide, upper Slite beds [SW48: 7]; SNO-DER VARIETY, **Hägsarve 6**, ditch and field outcrop of 'Hemse'-like shales (probably the time equivalents of the high *ludensis* Zone Klinteberg Formation around Snoder) on W side of road, ca. 900 m N of Snoder [SW103: 32]; **Hägsarve 7** (formerly Häxarve), drainage ditch of 'Hemse'-like shales on E side of road (high *ludensis* Zone 'Klinteberg' around Snoder), ca. 700 m N of Snoder, Br106527-8 [SW104: 16]; ?Näs, ?stratigraphic level as for Snoder localities, Br134620, [1].

Atrypa (Atrypa) affinis (James Sowerby, 1822)

Pl. 7, figs. a–q

- 1822 *Terebratula affinis* James Sowerby, fig. 324-2.
 1849 ?*Atrypa affinis*, Brown, pl. 44* [sic], fig. 3 (from Sowerby).
 1859 ?*Atrypa reticularis (affinis)*, Murchison, pl. 9, fig. 1; pl. 21, fig. 12 (same figure).
 1875 ?*Atrypa reticularis* Linnaeus, Baily, pl. 20, figs. 4a–b.
 1895 *Atrypa reticularis*, Reed, p. 502, fig. 331 [specimen A10205, Sedgwick Museum].
 1971 *Atrypa reticularis*, Earp and Hains, fig. 3, 2L.

Type locality and stratum. 'The specimens are from near Horncastle, and appear to be from decomposing Mountain Limestone . . . smaller ones have been sent to me from the Malvern Hills . . . and from Dudley' (as described by James Sowerby, 1822, p. 24; not J. de C. Sowerby). The Mountain Limestone is stratigraphically certainly in error, as it is of Carboniferous age; no Silurian outcrop is known at Horncastle. From fresh collections examined, the species appears to derive from the Much Wenlock Limestone (= *ludensis* Zone, latest Wenlock), but also occurs rarely in the lower 4 m of the Elton beds, i.e., lower *nilssoni* Zone. Cocks (1978) stated that *A. affinis* was from the Aymestry Limestone (lower Ludfordian, *leintwardinensis* Zone), but these specimens refer to *Atrypa sowerbyi*. J. de C. Sowerby (1839) identified it later as a Wenlock Limestone shell, with the additional remark, 'also Aymestry Limestone'. A specimen labeled as '*Ter' la affinis* 324, f.2 [sic: quoting J. Sowerby, 1822] in the British Museum (N.H.: BB61002), is a Devonian *Desquamatia*, probably *D. (Independatrypa) triangularis* Copper 1966, from the Eifel region, Germany. This specimen cannot be the original, and possibly came in exchange from Schlottheim Eifel material, which is also in the Natural History Museum (London). The name 'Parkinson' is mentioned as a source on one Geological Survey label (see also Parkinson, 1833). The Geological Survey collections of Sowerby contain two specimens labeled as *A. affinis*, GSM4151 and GSM4149: the former, GSM4151, is better preserved and very similar in size and form to pl. 6, fig. 5, of Sowerby (1839), and is herewith selected as lectotype. Like the Sowerby illustration, GSM4151 is somewhat damaged on the brachial valve. The label identifies it as coming

from the Wenlock Limestone at Dudley (not the Aymestry Limestone of Ludlow age). These suggest a range within the upper *ludensis* Zone. Similar specimens are known from the lower and middle Klinteberg Formation of Gotland (see Murchison, 1847, p. 21). I have also found it, although specimens are few, in the lowest 3 m of the Elton beds (early Ludlow). The type locality selected here is at Dudley, and the type stratum is probably from the upper part of the Much Wenlock Limestone.

Diagnosis. Large, ovoid *Atrypa*; nearly flat to weakly convex vv even in early growth stages, rounded shape and rounded hinge corners, 3–4 ribs per 5 mm, closely spaced growth lamellae (1.5–2.5 mm); broad U-shaped fold; frills absent or unknown.

Description. Large shelled (Much Wenlock variety widths 25–30 mm, Klinteberg 30–33 mm), widths about equal to length or slightly greater than length; vv relatively flat in the centre with slight rounding at the commissure, giving a weakly convex appearance; outline rounded, shield-shaped, flanks rounded with no clear hinge corner, hinge angle 130°–135°, shoulder line weakly indented. Lateral commissure relatively straight to weakly arched; anterior fold strong, U-shaped, highly arched in adult stages, weak in early stages. Beak protruding only slightly, blunt; area hypercline, hugging dorsal umbo; transapical foramen. Ribs strong, 3–4 per 5 mm, with only weak wavy growth interruption; growth lamellae numerous, relatively evenly spaced at about 1 mm, crowded anteriorly, protruding slightly away from shell; no frills observed. Interior structure not sectioned.

Remarks. The Much Wenlock Limestone species, *Atrypa affinis*, is coarser than *A. reticularis* in its rib spacing, and its ribs are more highly arched and clearly pronounced; it also has more closely spaced growth lamellae, and a more rounded, inflated dv. The species is most similar to *Atrypa lapworthi* Alexander (1949) from the lower Elton beds, but differs in its more rounded outline, clearly defined ribs, and short growth lamellae, and in its more inflated ventral umbo. *A. affinis* is relatively rare in Britain (it is most common in the Dudley area), and also in the Gotland succession probably because large *Atrypa* were not favoured in reefal environments. Murchison (1847, p. 21) mentioned the occurrence of '*Terebratula prisca* or *affinis*' in his unit 'H' from Klinteberg, and he was the first to recognize the distribution of the British species on Gotland. The species is distinguishable from *A. murchisoni* by its much larger size and coarser ribbing, and from *A. lapworthi* in its rib architecture and presence of a strong anterior fold. On Gotland and in the Wenlock Edge area, *Atrypa affinis* was associated with reefs, a relatively rare niche for the genus. Its more robust, thicker-walled shell, and high fold may have been an adaptation to reef habitats. It could be regarded as an ecological variant of other species, but even the earliest growth stages are distinguishable, and there is no gradational morphology where other species co-occur. Specimens from the Klinteberg Limestone tend to be somewhat larger (widths 32–33 mm) than British species (widths 25–28 mm). Curiously, Alexander (1949), in her revision of the British species of *Atrypa*, did not mention or select *Atrypa affinis* as one of the possible species, although it was commonly cited in the literature. Davidson's idealized illustrations (1867, pl. 14) of *Atrypa*

reticularis, under which he lumped *affinis*, are not clearly assignable to any species or specimens.

Materials. Total 45 specimens from the Much Wenlock Limestone, lowermost Lower Elton beds and upper Klinteberg Limestone. *Much Wenlock Limestone*: **Dudley**, BB34760 [3], BB3918 [8], BB23217 [2], A10205 [1], A26715-26 [12], A26675 [1], GeolSocColl GS4149 [1], GS4151 lectotype [1]; **Quarry west side Dudley Castle Hill**, A56747-56 [10]. **Wenlock Edge** BB608 [2]; **Dudley Castle Hill**, Wenlock Limestone, A30523-7 [5]. *Lower Elton beds*: **Shadwell Quarry**, calcareous shales about 2-3 m above Much Wenlock Limestone GB7 [12]. *Klinteberg Formation*: **Klinteberg 1**, Klinteberg sn., Br107929-30 [2].

Atrypa (Atrypa) lapworthi Alexander, 1949

Pl. 8, figs. a-v; Figs. 18, 19

1848 *Atrypa reticularis*, Davidson, p. 333, pl. 3, fig. 35 (vv, dv).

1949 *Atrypa reticularis* var. *lapworthi* Alexander, p. 214, pl. 10, figs. 3a-d [partim].

Type locality and stratum. 'Wenlock Limestone, Nacklestone, near Leintwardine, Herefordshire', Welsh Borderlands (Alexander, 1949), as for holotype A11623, Sedgwick Museum. This species does not appear to be present in the Much Wenlock Limestone, as it is developed to the north at Wenlock Edge, where it is common only in the lowermost few metres (1-3 m) of the Lower Elton beds. This suggests that perhaps the upper part of the 'Wenlock Limestone' at Nacklestone, Herefordshire, may be of lower Ludlow age. If this is correct, then the type stratum for the species may lie either within the *ludensis* or the *nilssoni* zones, or lowermost Ludlow. Abundant specimens similar to the type occur at the Shadwell quarry, 1-3 m above the top of the Much Wenlock Limestone contact (exposures in 1974; these were covered in 1989), and below the levels that contain *Atrypa murchisoni*.

Alternatively, the species may range downwards to the upper Wenlock in the Malvern Hills, and in younger rocks to the south. The tentative stratigraphic range of the species is late Wenlock to earliest Ludlow, thus possibly overlapping with the range of *Atrypa affinis* (Sowerby, 1822), and in the uppermost *ludensis* through lower *nilssoni* zones.

Diagnosis. Medium sized, averaging 20 mm wide, 10 mm deep, somewhat elongate, shield-shaped, with planar to weakly resupinate vv; ribs flattened, lacking frills or with very short frill; rectimarginate or with very weak fold.

Description. Shells ovate, convexoplane with vv planar to very weakly convex posteriorly to slightly resupinate at commissure; medium sized, ranging 20-24 mm wide (peak at 20 mm, maximum 30 mm), maximum widths posteriorly, longer than wide, depths 10-14 mm (peak 10 mm); distinctive shield shape; wide hinge angle (145°-150°); distinctive straight hinge, only faintly concave; well-defined hinge corners; lateral commissure very straight to weakly curved; commissure rectimarginate, anterior fold absent or weakly arched. Beak hypercline-adpressed, only slightly protruding over hinge; foramen transapical, small to absent even in very small shells; no deltidial plates observed. Ribs at 5-6 per 5 mm anteriorly, finer posteriorly in early growth stages; low, weakly defined to smoothed, continuous ribs, with very faint rise at growth interruptions (i.e., indistinctly wavelike); growth lamellae numerous, closely, evenly spaced at 1.0-1.5 mm, projecting at very slight angle away from shell; short frills (1-2 mm, rarely 3 mm), normally worn off during shell growth, only preserved along commissure; wide frills not observed.

Thick pedicle callist (no collar observed); teeth short, stubby, more dorsal than medial in direction, with poorly developed lateral lobes, minute dental cavities; dv with small cardinal pit, strong-moderate median septum; muscle scars weakly incised; projecting socket plates; bulbous inner socket ridges, moderate middle socket ridges; small rounded crural

Fig. 18. *Atrypa (Atrypa) lapworthi* Alexander, 1949. Scatter diagrams and frequency curves based on the holotype and specimens from the lower Elton beds, 1-2 m above the top of the Wenlock Limestone, Shadwell Quarry, early Ludlow; camera lucida sketch of adult shell.

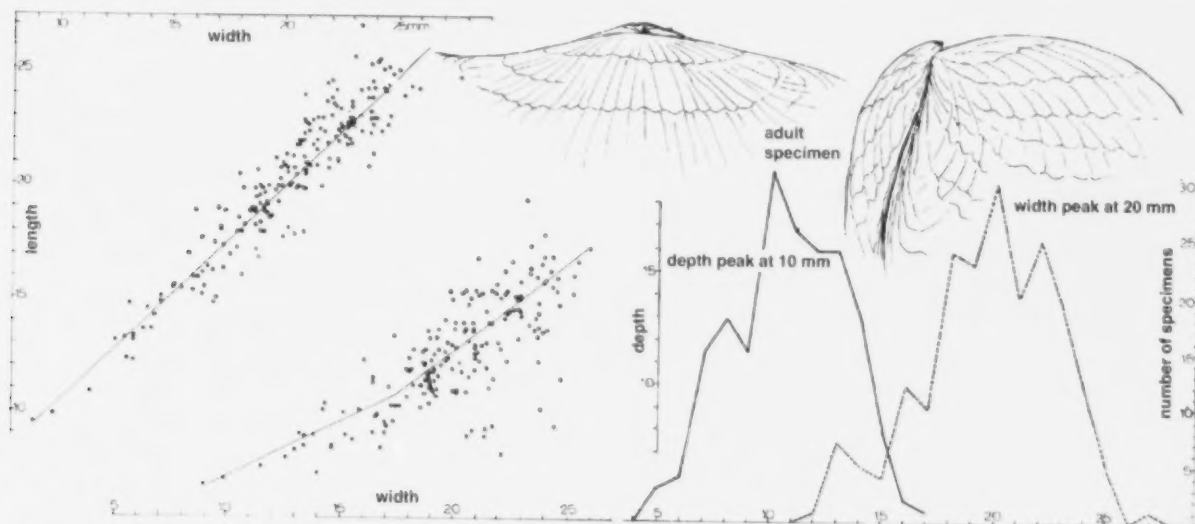
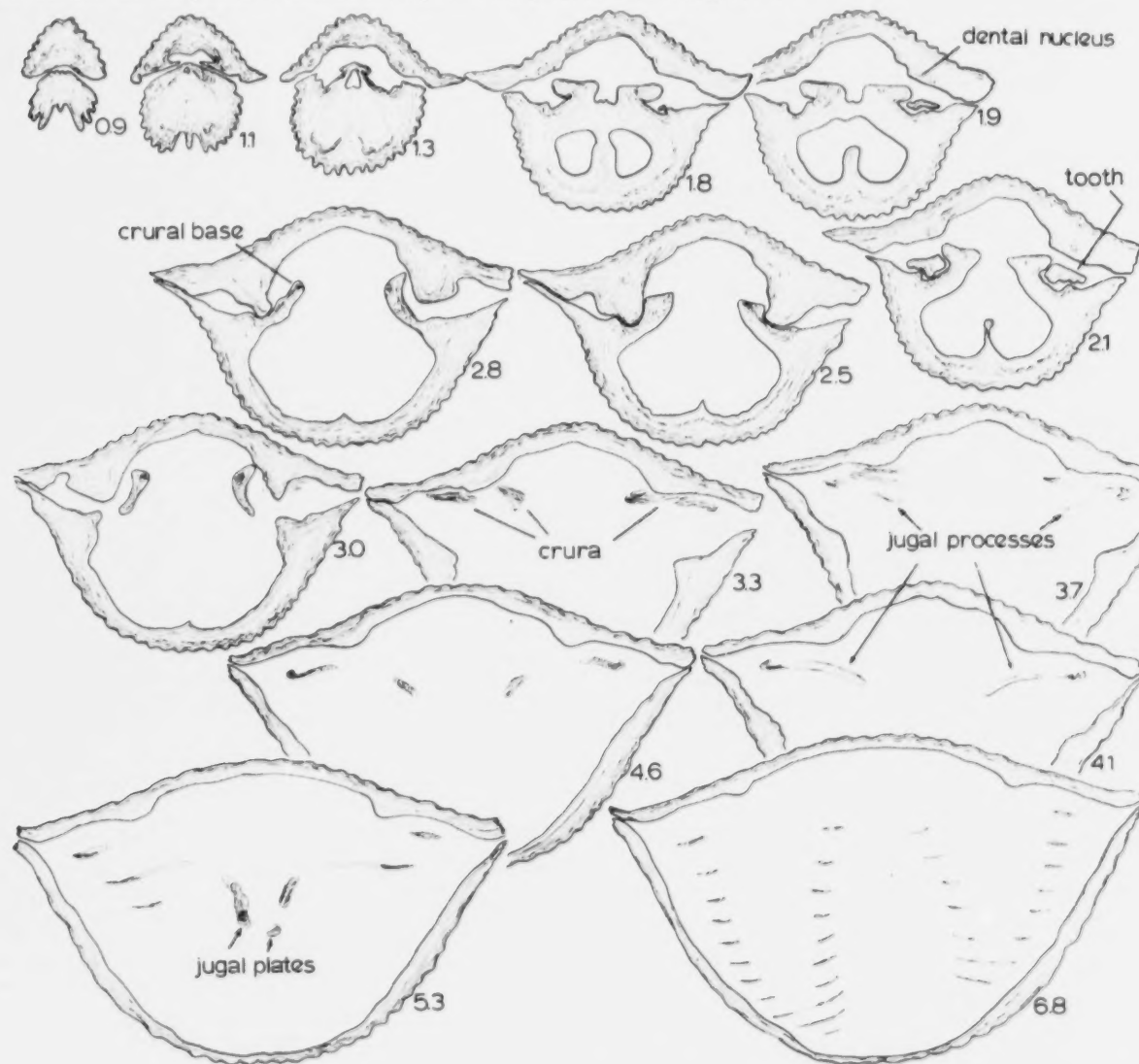


Fig. 19. *Atrypa (Atrypa) lapworthi* Alexander, 1949. Serial sections of specimen, Shadwell Quarry, lowest Elton beds, 1–3 m above Much Wenlock Lst., early Ludlow; note the development of jugal processes and jugal plates, $\times 4$.



bases: crura thick, feathered; jugal processes initially relatively straight, then curved medially, ending in long, vertical, thin structures; small, straight jugal plates; ca. 10 spiral whorls.

Remarks. This species is similar in size (only slightly smaller) and general shape to *Atrypa affinis* (Sowerby, 1822), from which it differs by having a flatter ventral valve, shield shape, a modestly weak fold, and ribs which are less tubular and less sharply defined. Possibly the two species are conspecific or intergrading, as seen in the illustrations of the original lectotype of *A. affinis* and comparisons with the type of *A. lapworthi*, but the boundaries between these species are finely defined. *A. affinis* is rather rare, occurring more commonly in Wenlock shallow peri-reefal and reefal limestones, with *A. munchisoni* primarily found in deeper facies Ludlow shales. It could be argued that *Atrypa affinis*, *lapworthi*, and *munchisoni* are simple facies variants which

reflect the deepening sea-level stands following the reefal buildups of the Wenlock Limestone. However, both *affinis* and *munchisoni* also occur in the Gotland succession at the same stratigraphic levels, which suggests that these species are not merely contemporary ecologic variants. Based on statistical comparison of more than 1700 specimens from the Shadwell quarry near Much Wenlock, *A. lapworthi* is almost exactly twice the average width (20 mm) and depth (10 mm) of the smaller-shelled *A. munchisoni*, which succeeds it in the Ludlow succession. *Atrypa reticularis* differs in having a flatter, wider shell, a well-developed anterior fold and frills. *Atrypa sowerbyi* has more tubular ribs, regularly and more widely spaced growth lamellae and frills.

Materials. 588 specimens. **Nacklestone**, Leintwardine, Welsh Borderlands, ?Wenlock Limestone, topotypic specimens from Alexander collection, A30515-22 [8]. **Shadwell Quarry**, east

side face (in 1975), Wenlock Edge, bedding plane layer in lower Elton beds, 1–3 m above top of Wenlock Limestone contact, GB7a [356], Gb20a [224]. This is the most abundant brachiopod in the basal layers of the Elton beds in the Shadwell Quarry; rare associated faunas include very large *Meristina obtusa*, small solitary rugosans, favositids, and heliolitids. The species is thus a faunal carry-over from the Wenlock Limestone below, as noted for other taxa by Shergold and Shirley (1968) and Shergold and Bassett (1970), who identified this species as *Atrypa reticularis*. The species is replaced higher in the Lower Elton beds by *A. purchisoni* [see below]. No similar specimens were found on Gotland.

Atrypa (Atrypa) purchisoni Alexander, 1949

Pl. 9A, figs. a–z, za; Figs. 20, 21

1949 *Atrypa reticularis* var. *purchisoni* Alexander, p. 215, pl. 10, figs. 4a–d [Ledbury].

1967 *Atrypa reticularis*, Brunton, Cocks, and Dance, pl. 2, figs. 26–27 [probably from Petesvik].

Type locality and stratum. 'Ledbury, Herefordshire, lower Ludlow Shales' (Alexander, 1949). This level is the equivalent of the lower Elton beds (Lower Ludlovian, *nilssoni* Zone), most likely from the now abandoned Ledbury quarry (SO 717:384), where it was said to be quite common. This species probably ranges through the middle to upper *nilssoni* Zone, but is possibly present as high as the *scanicus* Zone in Britain. Most of the material examined herein was from the Shadwell quarry, collected in 1974, at which time several almost monotypic shell beds were discovered in the lower greenish to dark grey soft-weathering shales. *A. purchisoni* tended to dominate a shell bed about 5–7 m above the Much Wenlock Limestone, above the horizon of *Atrypa lapworthi* Alexander 1949, and was scarcer in the lower layers. The associated fauna consisted of *Sphaerirhynchia*, large *Meristina*, cf. *obtusa* and lesser *Leptaena* sp.; corals, stromatoporoids, and calcareous algae were relatively scarce. The same shell beds were not clearly exposed in 1989 in the much larger quarry expansion. On Gotland, an identical form occurs at the Petesvik locality, in strata identified as lowermost Hemse (A) beds, and this shell appears also in

Fig. 20. *Atrypa (Atrypa) purchisoni* Alexander, 1949. Statistical variation in specimens taken from the Alexander collection and Shadwell quarry, 5–7 m above the base of Elton beds, early Ludlow; camera lucida sketches of neanic and adult specimen; width peak at 11 m, depth peak at 6 mm.

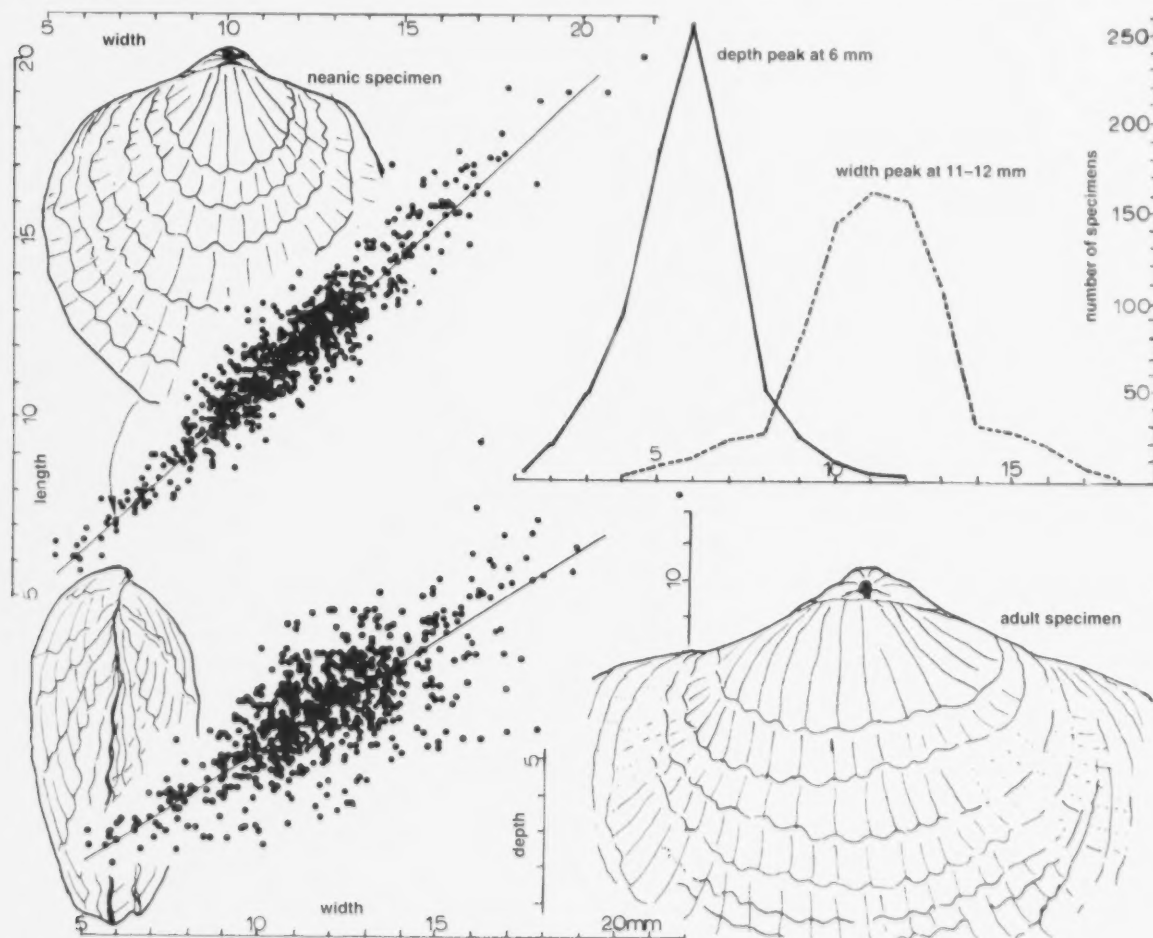
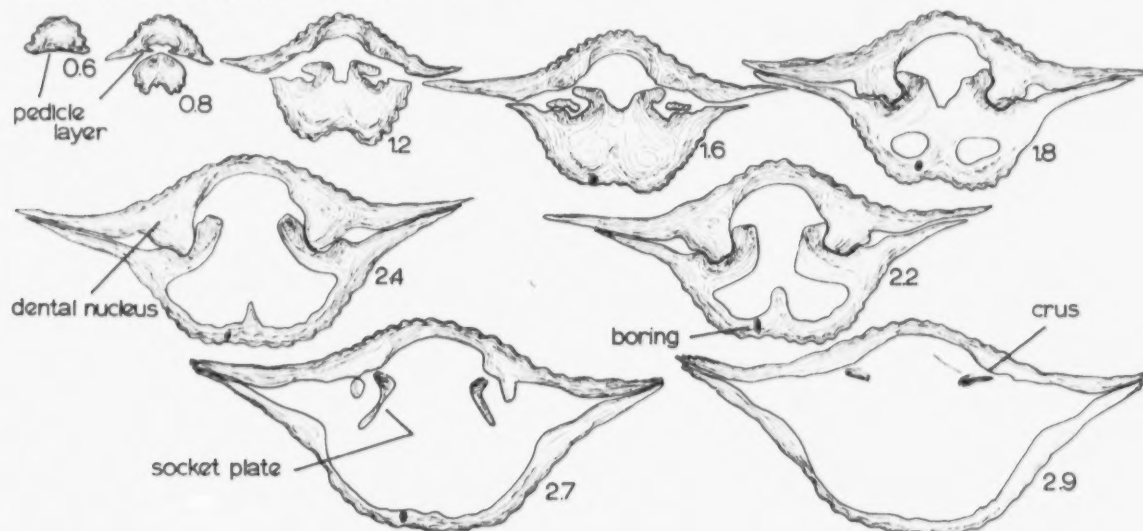


Fig. 21. *Atrypa (Atrypa) munchisoni* Alexander, 1949. Serial sections of specimen from Shadwell quarry, 5–7 m above base Elton beds, early Ludlow; spiralia and jugal processes not preserved; $\times 4$.



the Linnean type collections, suggesting that the Linnaeus "reticularis" collection came from several horizons.

Diagnosis. Small, averaging 10–12 mm wide, 6 mm deep, shield-shaped, dorsally inflated, convexoplane *Atrypa* with indented hinge line, and narrow, pinched anterior fold, very short growth lamellae.

Description. Shell small, about as long as wide or slightly longer than wide, average widths 10–12 mm (peak at 11 mm, maximum 19 mm), lengths 14–17 mm (peak at 14 mm, maximum 20 mm), depths 6–8 mm (peak at 6 mm); outline shield-shaped to somewhat triangular, globose; umbonal regions of vv weakly inflated and moderately convex, anterior regions of vv more flattened, often with small lip or concavity at commissure because of short frills; dv more convex to strongly inflated; lateral commissure weakly arched, deflected anteriorly by narrow, U-shaped, small fold; shoulder line weakly indented; hinge corners faintly defined to rounded; beak protruding only slightly; hypercline-adpressed area; foramen lacking, or, less commonly, small transapical. Ribs low, faint, fine at 7–8 per 5 mm, continuous, with only weak wavy interruptions; growth lamellae faint, numerous, closely spaced at 0.6–1.0 mm, somewhat deflected on vv in mature shells to form short frill about 2–3 mm long.

A distinct pedicle callist in the vv forms a thick pedicle collar; dental nuclei are small at the apex, absent anteriorly, teeth short, stubby, with lateral extensions; small cardinal process lining cardinal pit; hinge plate, inner socket ridges strong; socket plate thin, reinforced; crura laterally directed, fibrous (no spiralia and jugal processes in specimen sectioned).

Remarks. This species is common to abundant in Britain in the lower Ludlow Shales of the Silurian inliers in the Welsh Borderlands (esp. the Malverns), and in the Lower Elton beds, 5–7 m above the base. *Atrypa munchisoni* sometimes occurs, but rather rarely, with *Atrypa lapworthi* in the lowermost Lower Elton beds, and replaces it in the middle to

upper Lower Elton beds. It is similar to the latter, but *A. munchisoni* is smaller (about 50% smaller), has a more inflated ventral umbonal region (in early growth stages it is almost biconvex), and a narrow, pinched anterior fold. The question is whether the two species are merely ecological, stratigraphic or population variants, or valid species. The two species have a partly concurrent range zone in the Lower Elton beds, but *munchisoni* does not appear to occur in the Much Wenlock Limestone, and *lapworthi* is absent in the middle to upper part of the Lower Elton beds. They are here regarded as valid species because collections can be separated with a practiced eye, where they co-occur, and growth sequences, from small to large shells, form separate entities. *Atrypa munchisoni*'s shape, small size, and finer ribbing are identical to *Atrypa munchisoni* from the western facies of the lower Hemse beds at Petesvik. It should be noted that the Elton beds (ranging from 110 to 200 m thick: Shergold and Shirley 1968) represent a deepening sequence, and thus a smaller *Atrypa* species appears to have replaced a larger one during this transgressive phase. Tabulate (favositid, heliolitid) and solitary rugose corals very rarely co-occur with this species.

Materials. Total 1161 British specimens. Locus typicus, **Ledbury**, 'Lower Ludlow' shales, Herefordshire, Alexander collection, A30494 [1], A30577 [1], A30495–514 [19], A30325–6 [2]; **Lower Elton beds: Shadwell Quarry 1**, Wenlock Edge, loose collections in shales ca. 5–7 m above Wenlock Limestone contact, GB7b [221]; **Shadwell Quarry 2**, north side ledges, about 5 m above Wenlock Limestone, massive bedding plane surface collections in situ [GB20b: 918].

Total 266 Gotland specimens, mostly from around **Petesvik**, a distal shelf setting matching that of the Shadwell Quarry. The shoreline locality at the north end of Petesvik Bay has outcrops consisting of shaly bedding plane surfaces on the mudflats, from which fossils weather out. These are in the western facies of the lower Hemse For-

mation, basal Ludlovian, *nilssoni* Zone, lower Ludfordian. "Die Fauna von Petesvik-Hablingbo" [sic] was well known to Angelin and Lindström (1880; see also Jaanusson, 1986). A specimen from Petesvik is present in the Linnaeus type collection (see Brunton et al., 1967). Schmidt (1859, p. 437) first described the locality as consisting of a locality with "blue grey shales . . . scarcely 1–2 ft. above sea level . . . which through frequent action of flood waters, weathers fossils from the rocks". Van Hoepen (1910) mentioned the middle part of Petesvik Bay as being particularly fossiliferous. Associated fauna are almost entirely small, stunted brachiopods; especially abundant are small *Cyrtia*, *Howellella*, *Leptaena*, rhynchonellids, dalmanellids, trilobite fragments. Small, golf ball sized, hemispherical favositids are more common in the northwestern part of the bay. *Septatrypa petesvika* n. sp. occurs with *Atrypa murchisoni* at Petesvik. Lindström (1882, p. 19) had a list of other species from this locality. The nearest new locality is Lilla Hallvards 1, from which no collection was available. The species is very rare in the eastern, marginal marine, shallow facies of the Hemse beds (one specimen at Grogarns 4), where instead there are abundant *Atrypa sulcata* (Lindström, 1861). **Petesvik 1.** Hablingbo sn., Br104638-52 [15], Br104053-104100 [48]; **Sandskallen 3.** bedding plane flats exposed on northwest side of bay, 51 Hoburgen NO [SW100a: 156]; **Sandskallen 2.** north side of bay, bedding plane surfaces [SW100: 19]; **Petesvik 1A.** bedding plane surfaces, NE side of bay, near fishing huts at fence line [SW54: 48]; **Smissarve 4.** drainage ditch 2.1 km E of coast on road to Siglavjs [SW98: 12]; **Smissarvestrand 1.** small quarry bedding plane surface at shoreline [SW99: 7]; **Ocksarve.** dike 1.9 km NW Hemse church [1]; **Snaualds 2.** CJ 347 393, Br107973-77 [5]; **Visne.** Fardhem sn., kanalen fran Visne, Br43987-88 [2]; **Lojsta Klint.** Lojsta sn., Br47256 [1]; **Grogarns 4.** beach outcrop 1.2 km S of 's' in Grogarnshuvud [SW21: 1].

Atrypa (Atrypa) alata Hisinger, 1831a
Pl. 6B, figs. a–k; Figs. 22, 23

- 1831a *Atrypa reticularis* var. *alata* Hisinger, p. 120, 140–141, pl. 3, figs. 4 (dorsal, posterior views).
1831b *Atrypa alata*, Hisinger, p. 19 [from Näs].
1837 *Atrypa reticularis* var. *alata*, Hisinger, p. 75, pl. 21, figs. 11d–e [repeats 1831 illustration].
1974 *Atrypa reticularis*, Bassett and Cocks, pl. 9, figs. 2a–b [illustrates lectotype RMS Br2039].
1990 *Atrypa fumosa* Havlíček, p. 158–159, pl. 47, figs. 4–10.

Type locality and stratum. The original collecting locality was 'Vid vägen midt emot Näs Kyrka' (Hisinger, 1831a, p. 120). The Hisinger collection with this label has been examined (see Näskyra Materials). This is readily identifiable and comes closest to **Näs 1**, CJ 3404 3295 (Laufeld, 1974b). The type stratum is the western facies of the lower Eke Formation, probably only 2–3 m above the base, which is within the upper *Saetograptus leintwardinensis* Zone, or slightly above that level (early Ludfordian, middle to late Ludlow). Cherns (1982) indicated erosional surfaces and paleokarst at the top of the Hemse Formation and in the lowermost Eke Formation, which she marked as late *leintwardinensis* to *bohemicus* age. In the western outcrops, abundant *Atrypa alata* are associated with, and often covered by, *Rothpletzella* oncoids in the 'Sphaerocodium marls' of Munthe (1911; see also Copper, 1976). These cyanobacterial encrustations, made of an amalgam of calcified filamentous sheaths belonging to *Rothpletzella* and *Wetheredella*, commonly cover all or part of the shells at the Näs 3 locality, thus masking many atrypid specimens, which look like round balls. Other brachiopods encrusted include spiriferids and strophomenids, but atrypids dominated. At the same time, these contemporaneous oncolitic crusts preserve very fine details of the rib and growth lamellae ornament, and thus en-

Fig. 22. *Atrypa (Atrypa) alata* Hisinger, 1831. Statistical variation based on all specimens sampled from Näs 2 and Näs 3 localities, Eke beds, mid-Ludlow. Camera lucida sketches of neanic and adult shells.

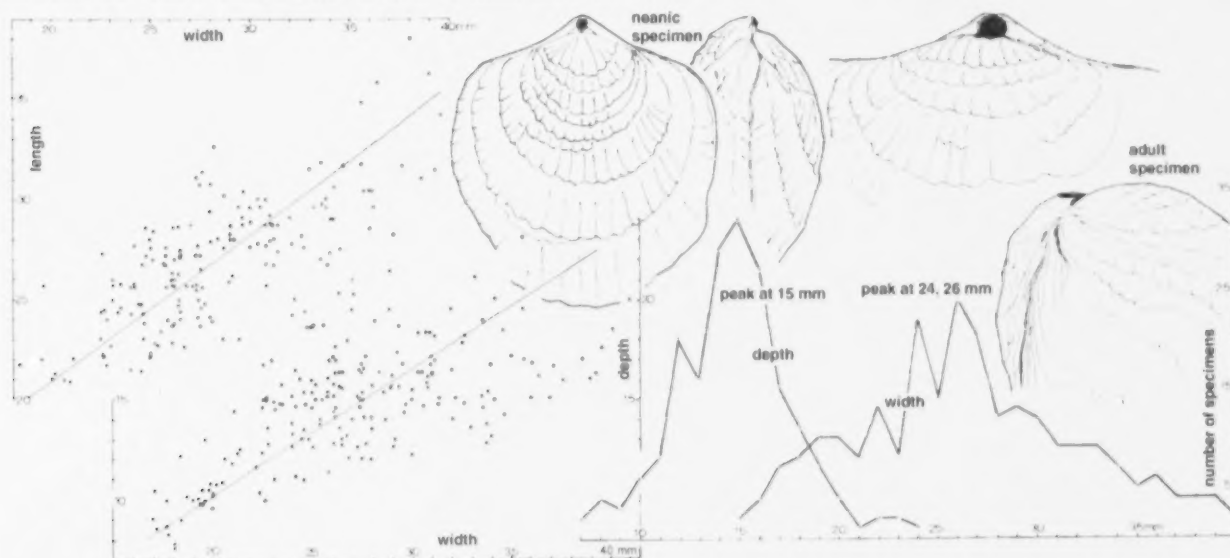
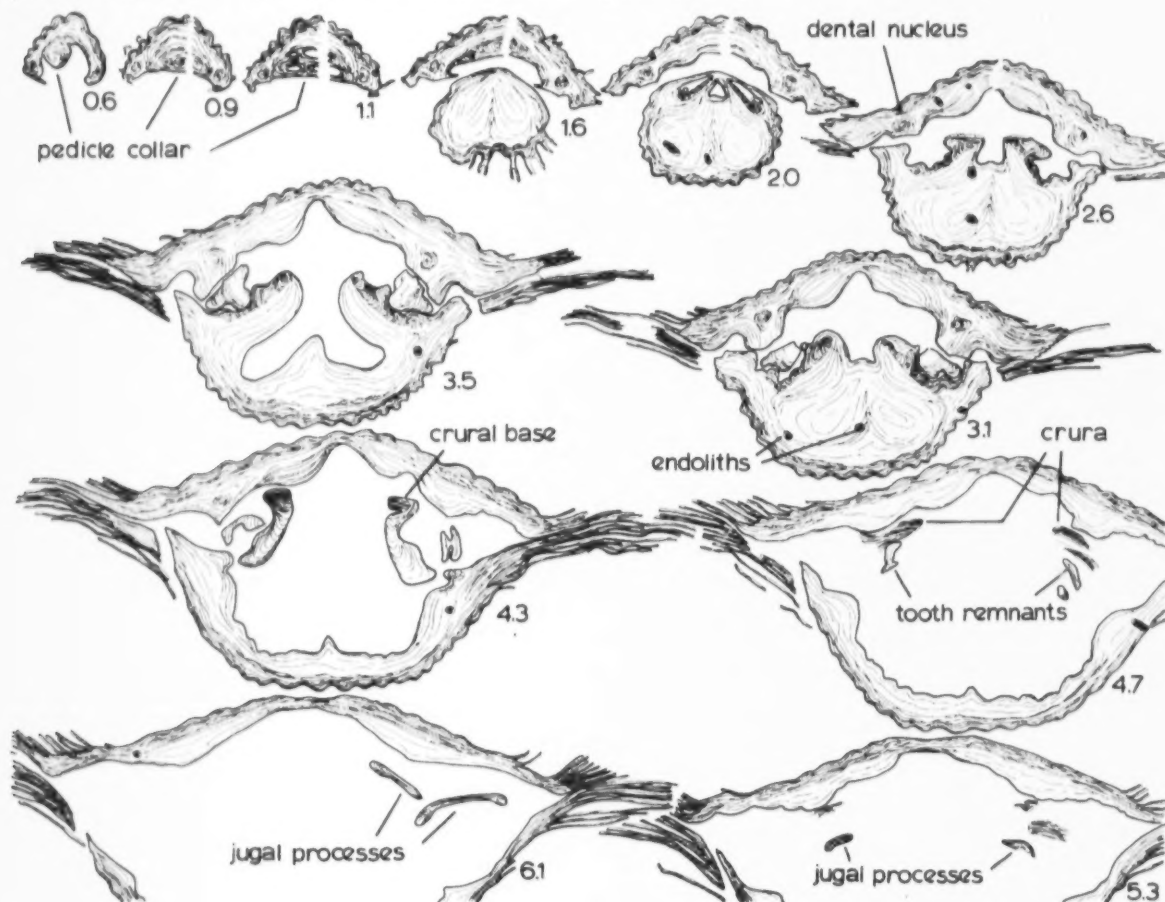


Fig. 23. *Atrypa (Atrypa) alata* Hisinger, 1831. Serial sections of typical shell from Näs 3, Eke beds, mid-Ludlow; apical ventral valve with post-mortem, pre-burial fractured, dorsal valve with numerous *Trypanites* borings; $\times 4$.



capsulated a picture of life on the sea bottom. *Atrypa alata* is absent in the central and eastern parts of the island, where '*Sphaerocodium*' occurs in encrusting domal to digitate porostromatolite forms (Cherns, 1982, 1983), and where higher energy marks another atrypid, *Endrea*. The oncolitic western 'algal' facies appears to indicate very shallow, periodically agitated shoals in the high subtidal zone. Many of the encrusted atrypids were bored by *Trypanites*. Storms may have carried live, whole *Atrypa* shells even into the intertidal zone, where they could have been covered by encrusting algae, but direct evidence for intertidal sediment is absent (e.g., mudcracks, salt casts, non-marine faunas). The shells are well preserved, having delicate growth lamellae intact. The paleokarst indicated to be present by Cherns (1983) was not observed where atrypid shells were found, suggesting that these shells did not fill in cavities on the karst surface.

Diagnosis. Relatively large shells, averaging 24–27 mm wide, 14–15 mm deep; usually with well-developed wide, densely packed, multiple overlapping frills at the commissure; growth lamellae at 2.5–4 mm; ribs coarse, somewhat flattened, smooth, at 4–6 per 5 mm.

Description. Large shells, early growth stages nearly biconvex, with shell somewhat elongated, later convexoplane-dorsibiconvex; maximum width 41 mm, average widths 24–30 mm, slightly wider than long (with frills preserved), lengths averaging 27–28 mm, proportionally not inflated, with depths averaging 12–16 mm, maximum depth 23 mm; apical angle 145° – 165° , dependent on frill preservation; hinge line weakly indented; beak adpressed; foramen transapical-apical, enlarged; deltidial plates lacking in adult growth stages, small in neanic stages. Ribs somewhat coarse, 4–6 per 5 mm (occasionally fewer), flattened at growth edges and interrupted, wave-like; growth lamellae systematically spaced at up to 4 mm, relatively wide apart in adult stages: frills wide, up to 6–8 mm from shell margin, overlapping densely at commissure, considerably adding to shell expansion where preserved; relatively narrow, angular V- to U-shaped adult commissural fold, rectimarginate commissure in early stages.

Shell wall relatively thick; ventral pedicle cavity closed by pedicle callist, developed into a single or double collar in some specimens; teeth somewhat short, blunt, nearly medially directed, with small dental nuclei, prominent lateral lobes; dorsal cardinal pit prominent, squared, lined by thin cardinal process spilling over onto inner socket ridges; hinge

plates strong, thick; socket plates thin; rounded inner socket ridges; crural bases apically small, distally expanding into wide, bushy crural fibres; jugal processes relatively thin; spiralia with up to 8–9 whorls.

Remarks. Many of the shells have a highly worn dorsal valve, with eroded ribs and growth lamellae, but a well-preserved ventral valve [when the shell is not coated by *Rothpletzella*]. Life position appears to have been invariably with the ventral valve down, based on observed field orientation, the presence of 1 mm diameter *Trypanites* borings, specimen wear, and appearance of the expanded foramen. Specimens from Näs 2 were statistically larger than those found at Näs 3, but this may have been due to collecting bias and inadequate sampling (less than 200 specimens).

The species most closely resembles *Atrypa slitea* from the northeastern facies of the Slite beds, but the latter is generally smaller, slightly more finely ribbed, possessing fewer overlapping growth lamellae, and with a more prominent U-shaped anterior fold. These two species together resemble, and anticipate, in their rib and frill development, the Devonian species-group *Atryparia* (Copper, 1966). The Devonian genus shows a much stronger tendency to lose its rib definition and increased frill expansion, and these Silurian species are closer to *Atrypa* (*Atrypa*) in their overall morphology. Hence they are retained in *Atrypa*. *Atrypa reticularis* is distinguished by its much finer ribs, more closely spaced growth lamellae, and shield-shaped outline. The Czech Ludlow species *Atrypa fumosa* (Havlíček, 1990) is almost identical in shape, size, and rib strength, and internal structure, perhaps lacking only the fading rib development: it is probably a junior synonym.

Materials. All 672 specimens came from the Eke beds, occurring along strike for a distance of about 20 km in south-west Gotland in the area around Näs. The species is the most abundant brachiopod of the western, shallow oncolite facies, although often obscured by oncoid overgrowth. The lectotype, Br2039, was selected from the Lindström collection by Bassett and Cocks (1974). No specimen like it is present in the Linnaeus type collection. **Näskyrka**, labeled 'vid vägen Näskyrka' (Hisinger collection of syntypes), Br2029–49, Br134692–4, Br124702–27 [50]; **Näs 2**, field outcrop 950 m NE Näs church, 150 m S intersection Klintehamn–Näs roads [SW30: 140]; **Näs 3**, field locality 530 m S of Näs church, 300 m NE Batels [SW31: 133]; **Skäls Café 1**, field locality opposite Skäls Café, E side of road [SW124: 223]; **Skäls 2**, field locality outcrop at wind turbine, 4 km SSW Olsvenne [SW125: 46]; **Bodudd 1**, beach outcrops N side Bodudd peninsula [SW126: 33]; **Sigsarve 1**, Br129116 [1]; **Kullunde 4**, no catalogue no. [6]; **Näsudden**, Br46933, 97, 99, 004 [4]; **Ronehamn 1**, 'dike vid järnvägsstationen', Rone sn., Br124685–701 [16], Br43354–55 [2]; **Ronehamn 2**, '500 m SV om hamnen', Br111340–42 [3]; **Petsarve 4**, Br11343–45 [3], Br107946–52 [7]; **Ronningskanal**, Grötlingbo sn., Br111368–9 [2]; **Eke 1**, Br104009–10 [2]; **Lingvide 1**, Br104011 [1].

Atrypa (*Atrypa*) *woodwardi* Alexander, 1949

Pl. 10A, figs. a–l

1949 *Atrypa reticularis* var. *woodwardi* Alexander 1949, p. 216, pl. 9, figs. 4–5; pl. 10, figs. 6a–d.

Type locality and stratum. 'Dayia navicula beds . . . Dinchope, near Craven Arms, Shropshire' (Alexander, 1949). These beds are of upper *leintwardinensis* through middle or late Ludfordian (late Ludlow) age, i.e., *bohemicus* through *formosus* zones: a more precise level is not assignable at present, since the collecting horizon is unknown. Around Dinchope a complete range of Ludlow strata are exposed (Shergold and Shirley, 1968). In Gotland, such shells occur in the Burgsvik Sandstone and Hamra limestones, but usually only as scattered, broken, probably transported valves, many disarticulated, and none are associated with *Dayia*.

Diagnosis. Elongate, ovoid, medium, convexoplane shells, 19–23 mm wide, coarse ribs 4 per 5 mm arc.

Description. Elongate-ovate shell, longer than wide (maximum width 30 mm, maximum depth 16 mm); moderately deep dv, flat vv; ribs relatively coarse; growth lamellae widely spaced at 3–4 mm; frills rarely observed as incomplete structures; hinge angles relatively narrow, ca. 100°–120°; hinge corners rounded, uncommonly subangular; anterior commissure gently plicate. Ventral valve interior with large, incised diductor scars, weakly distinguishable, small central adductors; vv shell wall relatively thick.

Remarks. *A. woodwardi* is similar to *Atrypa alata* Lindström 1861, but *A. alata* shows marked rib flattening, more widely spaced growth lamellae, and has an inflated ventral umbo. *Atrypa dzwinogradensis* Kozłowski 1929, from the late Ludlovian – 'Pridoli of Podolia, is most similar to this shell, differing only in a straighter hinge: it is possibly a senior synonym of the Alexander species. Alexander (1949) did not compare her species with those of Podolia, although she cited the Kozłowski reference. A statistical comparison is presently not possible because *Atrypa* is scarce in the Burgsvik through Hamra beds, and no statistics are available for the Podolian species. A re-analysis of the two species, based on additional material, is in order.

Materials. 41 specimens. Type locality, **Dinchope**, near Craven Arms, Welsh Borderlands, A11629 [holotype], A30535 [2]; **Greenways Cross**, Shropshire, A11627–29, A30536–42 [10]; **Burgsvik**, Öja sn., ?higher Hamra beds, Br42316–25 [10]; **Lundel** (Gansviken), Grötlingbo sn., abandoned quarries in lower Hamra beds, Br43430–35 [6]; **Hoburg**, v-sidan, märkeg., Br107978–9 [2].

Gotatrypa Struve, 1966

Type species. *Atrypa* (*Gotatrypa*) *hedei* Struve 1966, 'Gotland', Lower Visby beds, late Llandovery.

Range and distribution. This is primarily, and almost exclusively a mid- to late Llandovery (Aeronian–Telychian) shell, with a possible range into the early Wenlock. Species are widespread in North America, NW Europe, Kazakhstan, south China, and Siberia.

Diagnosis. Small to medium, globose, ventribiconvex to biconvex to weakly dorsibiconvex; minute, adpressed to hypercline area; foramen transapical or obscured by strong beak incurvature; deltidial plates absent in adult shells, but commonly present in neanic stages; fine to medium ribs inter-

sected by closely spaced, weak, wave-like growth lamellae, projected less than 2–3 mm, commonly pointed as sharp spines extended from the base of rib troughs, or as variable short lamellae; teeth with dental nuclei; crura thin, rarely bushy; short, centro-posterior jugal processes with small jugal plates; spiralia dorsomedial, fewer than 8–12 whorls. Internally, moderately thick pedicle callist (rarely a collar), teeth with dental nuclei, jugal processes terminating in blunt, spatulate tips; spiralia usually <10 whorls.

Distribution. Llandovery (Aeronian–Telychian) – ?early Wenlock, worldwide.

Remarks. The genus was originally erected as a subgenus of *Atrypa* by Struve (1966), but its distinctive biconvex shell, small size, and rib-growth lamellar structure warrant its elevation to independent genus status. It differs from *Atrypa* in its biconvex globose shape, and closely spaced, overlapping growth lamellae that commonly project as pointed spines along rib troughs. Indented muscle fields are very similar in both: most neanic specimens of *Gotatrypa* possess an apical foramen, and two minute deltidial plates. In some late Telychian *Gotatrypa* short frills up to about 5 mm long were developed. *Oglupes*, a descendant Wenlock–Pridoli genus, differs with very coarse to fading ribs, more equal biconvexity, and larger shell size; internal structure is very similar in both genera, although the pedicle callist is generally less well developed in *Gotatrypa*, and neanic *Gotatrypa* have an orthocline beak, and deltidial plates not seen in *Oglupes*. *Joviatrypa*, the probable ancestor of *Gotatrypa*, lacks growth lamellae, or has barely detectable lamellae, less than 0.5 mm long, and possesses a raised ventral muscle platform. *Protatrypa* differs in its relatively flat shell, and lacks short, distinct growth lamellae (see Copper, 1996b, for *Protatrypa* sections).

Struve (1966) identified the chief diagnostic characters as a small, dorsibiconvex shell (ventribiconvex in neanic stages) and finer ribs (7–16 per 5 mm) with closely spaced growth lamellae, but lacking frills (older species have coarser ribs). However, he also assigned other large, convexoplane species with frills, e.g., *Atrypa lindstroemi* (= *Atrypa sowerbyi*), here referred to as *Atrypa*. The biconvex nature of the shell, the absence of frills, and the presence of spine-like extensions along the rib troughs (where preserved) are distinctive external features of *Gotatrypa*. *Gotatrypa* is distinguishable from early to mid-Llandovery *Protatrypa* by its fine ribs, strong biconvexity, and in lacking a straight hinge and carinate flat vv with strong mid-rib pair. *Gotatrypa* differs from *Joviatrypa* (Copper, 1995) in the presence of growth lamellae, spine-like trough extensions, a hypercline to adpressed beak, and the presence of a depressed, rather than raised, ventral muscle field. From *Endreia* it differs in its finer rib structure, and lack of deltidial plates and orthocline area. Internally, its muscle pattern is like that for *Atrypa*, but it lacks its thick pedicle callist, has very small muscle scars (commonly somewhat raised at the margins), and feathered crura. It has only very short, stumpy jugal plates at the end of the jugal processes: no deltidial plates are known in adult shells.

On Anticosti Island, *Gotatrypa* is a common atrypid only in the Jupiter and Chicotte formations (late Aeronian – Telychian), and there are no true *Atrypa* present. This reveals

that *Gotatrypa* is primarily a middle to late Llandovery group: thus the Gotland occurrence is a 'dying gasp' for the genus. Nests of *Gotatrypa* reveal that it lived umbo down, probably with a small, functional pedicle protruding through the transapical foramen, or hidden under the incurved hypercline beak. *Gotatrypa* usually maintained only very short growth lamellae, as frills were not possible in an umbo down position (see also Seilacher and Meischner, 1964, who postulated a subvertical position for Llandovery *Protatrypa*). The evolution of extended frills in both *Atrypa* and *Oglupes* marked major innovation, transition, and adaptation for the Atrypidae, since earlier Atrypinae lack this development. *Atrypa* enhanced this trend by evolving a flatter ventral valve (convexoplane shell), allowing the shell to stabilize itself readily on the seafloor. The ancestor of *Gotatrypa* probably lies with the finely ribbed, unfrilled, biconvex–globose, Aeronian genus *Joviatrypa* (Copper, 1995), but differs in having extended growth lamellae, dental nuclei, and more *Atrypa*-like muscle scars and vascular markings.

Gotatrypa commonly co-occurs with *Oglupes visbyensis* in the Lower Visby beds, although the much smaller *Gotatrypa* shell is more abundant. *Gotatrypa* appears to end in the Lower Visby beds on Gotland: it is a genus apparently confined to rocks of Llandovery age (but there are questionable reports of early Wenlock forms: see below list). Species assigned to *Gotatrypa* here have also been referred elsewhere to *Nalivkinia*, *Protatrypa*, and *Gruenewaldtia*.

Species assigned.

- Atrypa septentrionalis alia* Nikiforova 1961, Tunguska River, Siberian Platform, Telychian, Llandovery.
- Atrypa hedei americensis* Sheehan 1982, Barn Hills, Utah, Laketown Dolomite, Telychian, Llandovery.
- Atrypa antiqua* Kulkov 1989 [in Kulkov and Severgina], Inya River, NW Altai, Sirovatn Suite, Chinetskin Horizon, ?middle Llandovery.
- Atrypa gabrielse* Norford 1962b, B.C., Canada, Sandpile Group, Telychian, Llandovery [see also Norford, 1962a].
- Protatrypa inflata* Beznosova 1985, Sharyu R., Komi Republic, Russia; ?Wenlock.
- Nalivkinia jartasensis* Andasheva 1980, Jartas River, Siberia, Telychian, Llandovery.
- Protatrypa lepidota* Nikiforova and Modzalevskaya 1968, Rynoi R., Siberian Platform, ?Wenlock.
- Gruenewaldtia nalivkinoidea* Borisyak 1955a, Karagandin region, Kazakhstan, ?Wenlock.
- Protatrypa olga* Kulkov 1967, Kamysheh, N Altai, Chagyr beds, ?Wenlock.
- Atrypa orbicularis* J. de C. Sowerby 1839, Gorrllwyn-Fach, Wales, Telychian, Llandovery.
- Protatrypa* (?) *polymorpha* Beznosova 1985, Kozhim River, Prepolar Urals, Llandovery.
- Atrypa septentrionalis* Nikiforova 1961, Gorbityatchin River, Siberia, Llandovery.
- Atrypa subquadrata* Rybkina 1985, W Tuva, Ara-Arga beds, Telychian, Llandovery.
- Protatrypa thorslundii* Boucot and Johnson 1964, Jämtland, Sweden, Ede Quartzite, Llandovery.

Gotatrypa hedei Struve, 1966

Pl. 11A, figs. j-s; Figs. 24, 25

1957 *Atrypa reticularis*, Jux, p. 59, fig. 4-21.1966 *Atrypa* (*Gotatrypa*) *hedei* Struve, p. 130-133, pl. 15, figs. 4-6.1967 *Atrypa reticularis*, Brunton, Cocks and Dance, pl. 2, fig. 24.1970 *Atrypa hedei*, Rubel, pl. 20, figs. 2-11, 22.1982 *Atrypa* (*Gotatrypa*) *hedei*, Copper, p. 684, fig. 3.

Type locality and stratum. 'Kap Gnisvård etwa 14 km NNW Klintehamn . . . Obere Visby-Mergel' (Struve, 1966, p. 130). The Struve locality is probably the same as **Gnisvård 1** (Laufeld, 1974), although the precise collection of material studied by Struve is not known, since it was based on museum collections. The Gnisvård 1 locality was the result of excavations for the harbour, and loose specimens still occurred there in the 1970s. The horizon 'Obere Visby Mergel' identified by Struve is certainly incorrect, as this species only occurs in the Ygne Mbr. of the Lower Visby beds, *Monoclimacis crenulata* Zone (late Telychian). The species is widespread and not uncommon in the Lower Visby beds, ranging from Gnisvård in the SW to Nyhamn in the NE, 18 km NE of Visby. In the Lindström collections at the Riksmuseet, this species was informally listed and cited by Lindström as '*Atrypa concinna*', but this remains an undescribed nomen oblitum, although it precedes Struve's usage.

Diagnosis. Small, rounded to ovoid, biconvex to dorsibiconvex with weak anterior fold; very fine ribs, short overlapping (<2 mm) growth lamellae; vv with slightly raised central mid-ribs; beak hypercline; foramen minute, commonly obscured, transapical, or covered; deltidial plates absent; pedicle

callist thick; minute but distinct dental nuclei, dental cavities minute or absent; muscle scars incised small, commonly with raised anterior rims, almost platform-like; thick hinge plate; crura non-fibrous; jugal processes tipped by stumpy, very short jugal plates; spiralia with 6-8 whorls.

Description. Small, shield-shaped shells, slightly wider than long, widths averaging 13-15 mm (peak at 14 mm), length 12-14 mm, depths 7-8 mm (peak at 8 mm); dorsibiconvex with somewhat more weakly convex ventral valve; weakly indented shoulder line; rounded hinge corners; gently arcuate anterior dorsal fold; ribs very fine, 13-14 per 5 mm, slightly demarcated by wavy rib rows; growth lamellae short, barely extending 2 mm beyond shell, commonly crowded anteriorly and overlapping; rib rows and growth lamellae spaced at 0.2-0.7 mm (most in the lower range), only weakly developed; growth lamellae extended as peaks in rib troughs; foramen commonly transapical, minute (<1 mm diameter), or covered by hypercline beak; no pedicle collar. Ventral valve interior with callist; dental nuclei distinct, laterally expanded into small or minute dental cavities; teeth short, blunt, with weak lateral lobes, directed at 45°; cardinal pit small, rounded to V-shaped, lacking cardinal process; hinge plate thick; socket plate thin, arcuate; inner socket ridge rounded, lobed; middle socket ridge small; crural bases small, rounded expanding into ventral cavity as horizontal blades (no feathering seen); jugal processes horizontal, arcing gently into central-dorsal cavity in a vertical position, terminating in short, stubby jugal plates; spiralia dorsally directed, with 6-8 very thin whorls.

Remarks. The species readily distinguishes itself from contemporaneous *Oglupes visbyensis* and *Atrypa* (*Atrypa*) *gotha* n. sp. by its much smaller size (less than one third wide),

Fig. 24. *Gotatrypa hedei* Struve, 1966. Statistical comparison of shells combined from various localities, all from Lower Visby beds, Ygne Mbr., late Llandovery. Camera lucida drawing of shell apex, Br104112, Kinner, ca. $\times 8$.

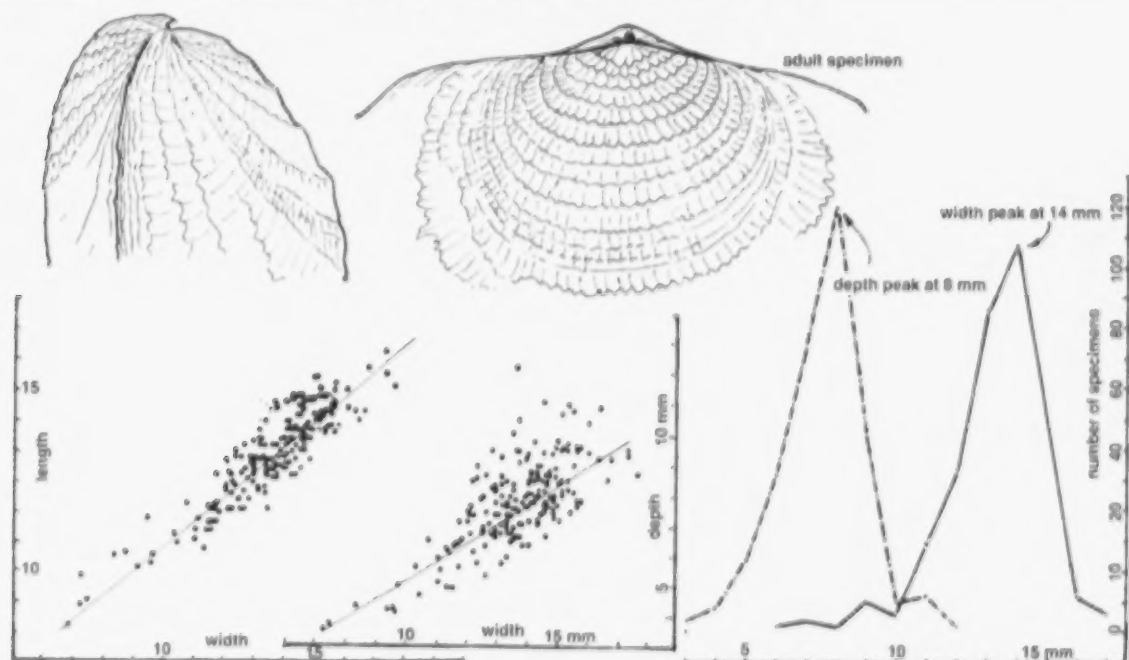
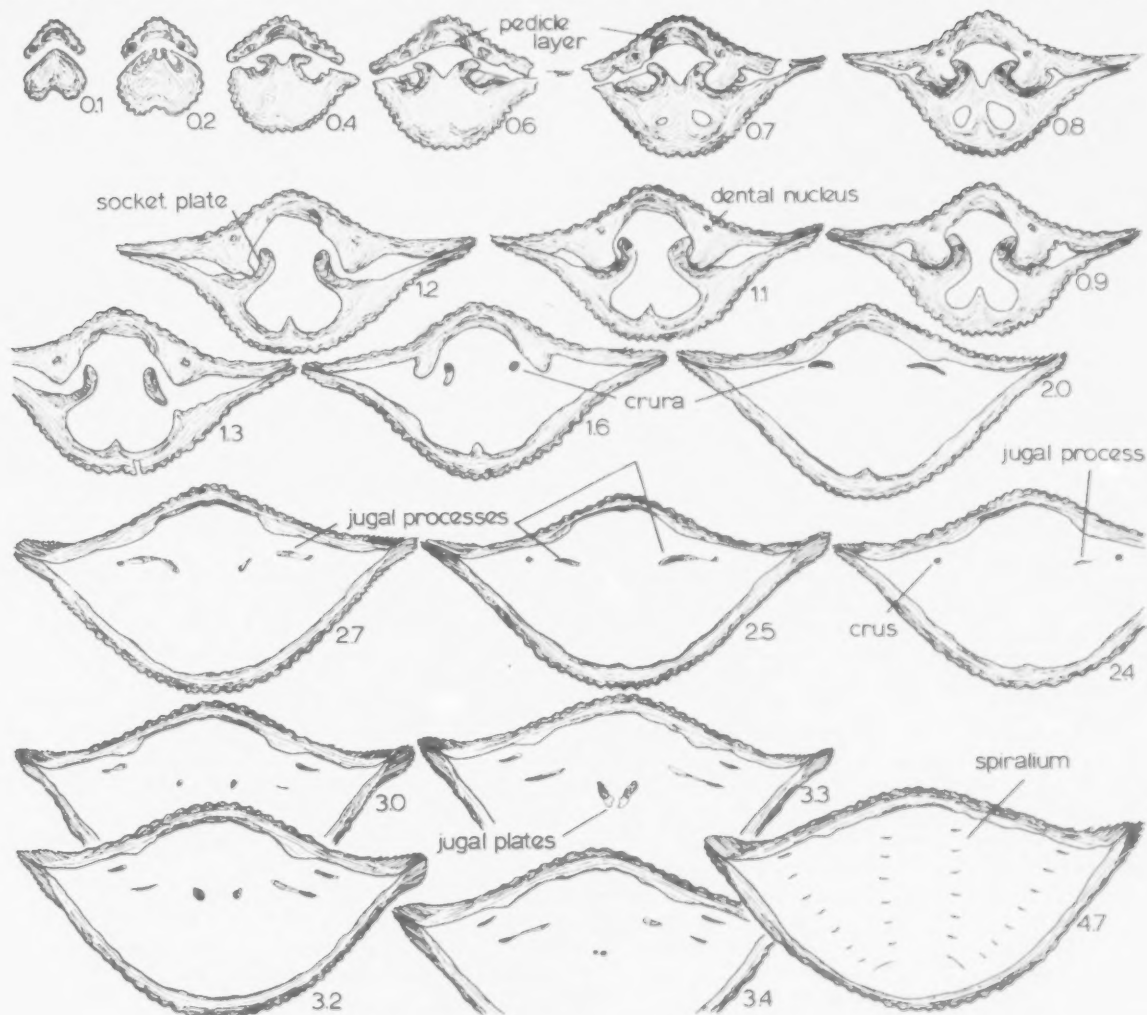


Fig. 25. *Gotatrypa hedei* Struve, 1966. Serial sections of typical specimen, Br108034. Lower Visby beds, 'Visby', late Llandovery, *5.



and very fine ribs. Even neanic specimens are readily distinguishable, with *Atrypa* being convexoplane and coarsely ribbed at that size, and *Oglupes* being large, more coarsely ribbed, and strongly biconvex. The type species *G. hedei* is one of the last species in the lineage, and shows trends towards shell flattening and adoption of a vv down position not seen in earlier Llandovery species.

Materials. 89 specimens. Lower Visby shale, **Kinner**, 'hall vid stranden V om Kinner' (near Nyhamn 3), 06600:55200, Br104107-122 [16]; **Nyhamn**, 07400:55300, Br104123-26 [4]; **Gnåsvärd 1**, 77700:38300, Br105056-57 [2], Br104015-16 [2]; **Gnåsvärd 1**, loose collection on N side of harbour [SW8: 4]; Visby **Norderstrand**, 95000:49300, Br10830-38 [9]; **Visby**, Br108015-34 [19]; **Lusklikt**, 'N om Lusklikt understa lage, circa 2 m o.h.', 08800:55700, about 2 km NE of Nyhamn, Br107924 [1], Br107864-69 [7]; **Gustavsvik**, 'Udden N om Gustavsvik', Br107872 [1]; **Rönnklikt**, 11800:56950, Br107919 [1]; **Garnudden 9**, shale exposures low on beach on the N side of Rönnklikt [SW37: 6]; **Gus-**

tavsvik 1, about 3 km NE of Visby centre, thin shale exposure along beach [SW2: 8]. This is quite a common, although not abundant, species in the soft-weathering, clayey shales of the Lower Visby shales, and many may be collected at some localities, where it is probably overlooked due to its small size.

?Gotatrypa orbicularis J. de C. Sowerby, 1839
Pl. 9B, figs. 9a-e

1839 *Atrypa orbicularis* Sowerby, p. 737, pl. 19, fig. 3 (4?).

Type locality and stratum. 'Gorllwyn-fach' (Sowerby, 1839), near Llandovery, Dyfed; Telychian (late Llandovery, C4). Cocks (1978, p. 156) selected a lectotype from the Sowerby collection in the Geological Survey Museum, London, GSMGsd6073, a sandstone steinkern of a decorticated shell. The second specimen, consisting only of external moulds, illustrated by Sowerby (1839, pl. 19, fig. 4), was not discov-

ered in the collection. No other specimens were available from the type locality.

Diagnosis. Medium sized, rounded, ca. 17–18 mm wide, about as wide as long, ca. 9–10 mm deep, globose, biconvex, rounded; shell surface covered by moderate ribs, 7–8 per 5 mm arc; weak vascular canals extend from line within ventral diductor field; gonadal pits deeper on ventral valve; dorsal muscle field divided by moderate, short septum.

Remarks. No other description can be provided at this time, as the species appears to be poorly preserved in the British sections, occurring only as moulds, and no fresh material was available from old or new collections. No information is available as to whether the type is a large or immature individual, or whether it has frills or only short growth lamellae. The specimens can only be broadly assigned to *Gotatrypa* on the basis of its shape, convexity, and rib structure (it could be a smaller *Oglupes*). It is almost impossible to identify atrypid species on the basis of moulds and casts, thus disregarding critical internal structures. The type specimen has been photographed for comparison with the oldest species on Gotland, *Gotatrypa hedei* Struve 1966. The species is absent on Gotland, as no Telychian rocks of that age are exposed. A probably conspecific species, very similar in shell shape and rib coarseness, and several other species occur in great abundance in rocks of the middle to upper Jupiter Formation on Anticosti island (Llandovery, late Aeronian–middle Telychian), and this material will be compared and described in a monograph under preparation. The Llandovery shells lack all traces of frills, and possessed only very short growth lamellae, usually less than 1 mm in extent. This is similar to *Protatrypa* Boucot and Johnson 1964, which differs, however, in having ventral carination, a wide flattened shell, and a relatively straight hinge. Thus it appears that distinctive frills were not really developed until late Llandovery time, about the same time as the evolution of the flat pedicle valve of *Atrypa*. Rybákina (1985) illustrated a species from Tuva, *Atrypa subquadrata*, which is much like other Atlantic Llandovery forms resembling *A. orbicularis*. Thus such related forms may be widespread.

Oglupes Havlíček, 1987

[= *Kantinatrypa* Havlíček, 1995]

Type species. *Oglupes scarabeus* Havlíček, 1987b, p. 240; OD.

Range and distribution. Late Llandoveryan to Pridolian = Lochkovian; worldwide.

Diagnosis. Small to large, biconvex–dorsibiconvex; hypercline–adpressed, obscured area; small beak; foramen absent; ribs relatively coarse; surface bearing distinctive, fine concentric filae, with concentric growth lamellae, frills, or trail; anterior commissure rectimarginate to weakly plicate; pedicle callist moderate; deltidial plates absent; teeth with possible dental nuclei; cardinal process minute to absent; socket plates thin, with strong inner socket ridges; spiralia up to ca. 12 whorls; jugal processes small, slender, apparently lacking jugal plates.

Description. Biconvex to ventribiconvex, less commonly dorsibiconvex, often globose *Gotatrypa* with medium to coarse ribs, medium-sized to wide frills; hypercline beak; small

orthocone area; apical–transapical foramen; pedicle callist well developed; pedicle collar common; deltidial plates absent; teeth with dental nuclei; small relatively slender jugal processes nearly touching; spiralia with up to 12 whorls in large species.

Remarks. *Oglupes* is externally distinguished from *Gotatrypa* by its growth of prominent frills (where these are preserved), and the development of bigger shells, and coarser ribs. This genus accompanies the smaller, related, probably ancestral genus *Gotatrypa* in the Lower Visby beds, but reaches its main distribution in the Upper Visby strata on Gotland and higher, where *Gotatrypa* is absent (and appears to have become extinct). Where frills are lost or not preserved, the ragged tear margins are usually evident. In *Gotatrypa* the growth lamellae are commonly extended as short spines along rib troughs, whereas this is not seen in *Oglupes*. The ribs in some *Oglupes visbyensis* also show strong flattening, but considerable variability seems to exist in the early species. Internally, *Gotatrypa* generally has a more incised ventral muscle field, with a raised anterior lip, and two very prominent, raised, parallel ventral vascular canals extending anteriorly from the outer posterior margins of the diductor muscle field. Since very few Llandovery *Gotatrypa* have been sectioned, there may be other internal criteria to distinguish these shells. Struve (1966) stated that *Gotatrypa* was distinct because of its exceptionally fine ribs (7–16 ribs per 5 mm of arc) and small size: this appears to be true for most species. The frilled genus *Atrypa* may have evolved from frilled *Oglupes*, with a split between the two genera occurring very early, probably in late Telychian time: the two taxa are almost concurrent on Gotland, although *Atrypa* is rare in the late Telychian. By the *Gothograptus nassa* Zone, in the beginning of the Homerian, after Mulde Marl deposition, *Oglupes* appears to have disappeared from Gotland. This may be attributed to the local loss of deeper water habitats on Gotland in the Ludlow. A similar loss is seen in the British succession, which continues with *Atrypa*-rich, deeper water facies through the Elton beds. Thus the disappearance of *Oglupes* is perhaps more widespread in the area.

Oglupes scarabeus Havlíček 1987, the type species of *Oglupes*, from the Motol Fm. (Wenlock) of the Czech Republic, was originally described as having frills. Havlíček (1995, p. 58) later regarded that this was in error and that the type species lacked both frills and growth lamellae, but this is now seen to be incorrect, with the original diagnosis being valid. He then added another genus, *Kantinatrypa* (type *K. gambrina* Havlíček 1995), for forms that had frills: this seems a poor criterion, as identification would then depend solely on frills. Several species assigned by Havlíček (1987b, 1995) to *Atrypa* are better assigned to *Oglupes*, as Havlíček regarded *Atrypa* as having a biconvex shell, whereas its adult shell is convexoplane. *Atrypa* also differs in having ribs arranged in waves that weaken at the frill breakage point, and in having perforated frills: these are unknown in *Oglupes*. The Gotland material indicates that the presence or absence of frills in such shells is a taphonomic feature of post-mortem breakage, or collecting breakage, as the shell frills may detach or weather away prior to collecting. All other features of the shell appear the same.

Oglupes appears to be a branch in the evolution of the Atrypinae, producing larger, biconvex shells with frills. In

early growth stages *Atrypa* may also have a biconvex shell, but this shell is usually flattened, particularly the vv, in its overall shape, whereas *Gotatrypa* and *Oglupes* have globose, biconvex shells. *Oglupes* is difficult to separate from Devonian *Kyrtatrypa* Struve 1966 [= *Tenuiatrypa* Rzhonitskaya 1975]. Struve (1966) suggested that *Gotatrypa* was more finely ribbed, had growth lamellae which were much more closely spaced and a more even sculpture. The first two features mentioned appear to be valid; the third, however, is difficult to identify. Havlíček (1990) mentioned that *Oglupes* is distinct from *Atrypa* in lacking a pedicle callist (or pedicle collar), but this is not fully developed even in all species of *Gotatrypa*, and in Gotland *Oglupes* a pedicle callist is well developed. Havlíček (list below) described 10 species of *Oglupes* from the Prague Basin (5 from the Kopanina and 5 from the Motol formations of Wenlock and Ludlow age).

Species tentatively assigned to Oglupes.

- Atrypa alba* Lamont 1978, Gutterford Burn, Scotland, 'silty limestone', late Telychian, Llandovery.
Atrypa reticularis alexanderi Chiang, 1972, Kemble, Ontario, Amabel Fm., Wenlock.
Gotatrypa copperi Havlíček 1990, Prague Basin, basal Kopanina Fm., early Ludlow.
Protatrypa crasscostata Su 1976, Dalhanmaomingan, Lianheqi, Inner Mongolia, Bateobao Fm., Ludlow.
Atrypa reticularis var. *davidsoni* Alexander 1949, Woolhope Limestone, Malverns, U.K., middle Wenlock.
Atrypa reticularis var. *depressa* Borisyak 1955b, Chingiz Range, Kazakhstan, late Telychian, Llandovery.
Atrypa evanida Havlíček 1990, Prague Basin, upper Kopanina Fm., late Ludlow.
Atrypa fumosa Havlíček 1990, Prague Basin, lower Kopanina Fm., Gorstian, early Ludlow.
Kantinatrypa gambrina Havlíček 1995, Prague Basin, Kopanina Fm., Ludlow.
?Atrypa gibbosa Hall 1852, Clinton, New York, late Llandovery – early Wenlock (has frills).
Atrypa gibbosa Kazanski 1899, Sims River, near Serpevka, Urals, ?Ludlow.
Atrypa margarita Barrande 1879, Prague Basin, upper Motol Fm., late Wenlock.
Atrypa jartasensis mongolensis Rozman 1988, Mongol Altai, Yokusin beds, Wenlock.
Oglupes muldea n. sp., Mulde Brick Quarry, Gotland, Mulde Marl, late Wenlock.
Atrypa orientalis orientalis Rozman 1988, Mongolian Altai, Salkhitin beds, early Wenlock.
Atrypa orientalis grandis Rozman 1988, Mongolian Altai, Yokusin beds, late Wenlock.
Atrypa praefumosa Havlíček 1995, Prague Basin, upper Motol Fm., Wenlock.
Atrypa petrotella Amsden 1978, Oklahoma, Quarry Mountain Fm., middle Wenlock.
Oglupes scarabeus Havlíček 1987, Prague Basin, Motol Fm., late Telychian – Wenlock.
Gotatrypa scabricosta Havlíček 1991, Prague Basin, upper Motol Fm., Wenlock.
Protatrypa sinuata Su 1976, Dalhanmaomingan, Lianheqi, Inner Mongolia, Bateobao Fm., Ludlow.

"*Eocoelia*" *smydra* Havlíček 1995, Prague Basin, middle Motol Fm., middle Wenlock [= neanic *Oglupes*].

Atrypa tokrauensis Olenicheva 1983, Pribalkhash, Kazakhstan; Tokrau Horizon, Ludlow.

Atrypa turensis Mizens 1977 [= *O. davidsoni* (Alexander 1949)], Central Urals, Tura river, Elkino, Wenlock.

Atrypa vanicosta Havlíček 1991, Prague Basin, upper Kopanina Fm., late Ludlow.

Oglupes visbyensis n. sp.

Pl. 12, figs. a–t; Pl. 15B; Figs. 26, 27

1868 *Atrypa reticularis*, Davidson, p. 12–13, pl. 1, figs. 18–21, 'Wenlock Shale, beds D–E', Pentland, Scotland.

1966 *Atrypa (Atrypa)* sp., Struve, p. 141, fig. 8.

1970 *Atrypa hedei* Struve 1966, Rubel, pl. 18, figs. 1–19; pl. 19, figs. 13–16.

Type locality and stratum. **Stavsklint 2:** the strata from which the specimens were collected are about 4 m above sea level in the bluffs stretching along the coast at Stavsklint (Tofta Skjutfält), 6l Visby NO 83600–83850:39250–39350 [I thank Colonel Lennart Ström and his wife Pat, for leading me to these cliffs, not normally accessible]. This level is in the upper part of the Lower Visby beds, Ygne Member. The species, however, ranges from lower in the Lower Visby beds, where it accompanies the very small species *Gotatrypa hedei*, through the Upper Visby beds (Rövar Liljas Member), where *Gotatrypa* is absent. These specimens normally occur away from the Axelro patch reefs or reef margins. The probable range of this species is from the upper *crenulata* through middle *murchisoni* zones, spanning the Llandovery–Wenlock boundary.

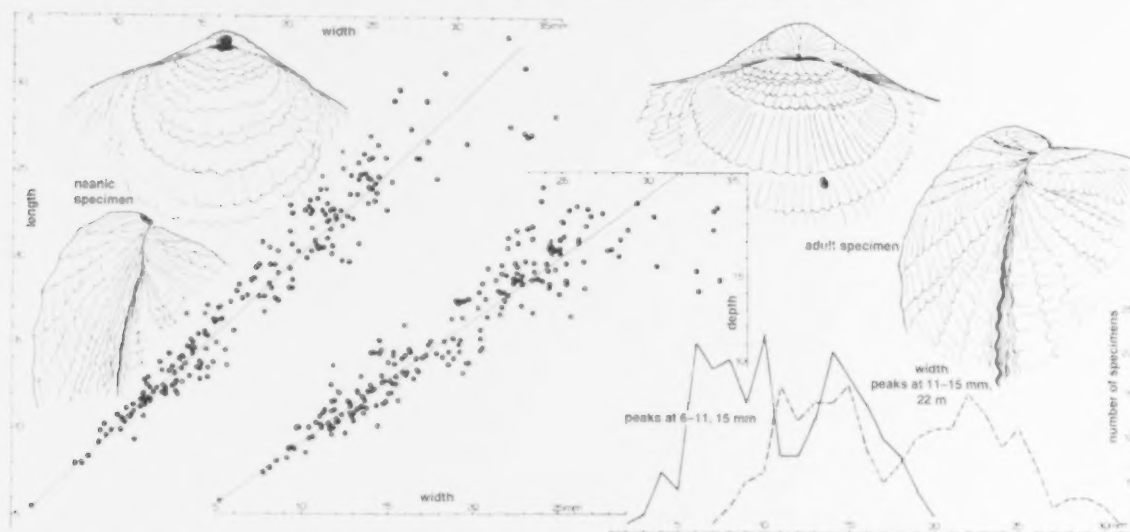
Diagnosis. A very strongly inflated, large (to 35 mm), biconvex, globose, inflated shell with long and prominent frills, moderately coarse ribs.

Description. Ovoid, usually strongly biconvex–dorsibiconvex shells, averaging 20–25 mm wide (maximum 35 mm, with frills), usually longer than wide, 14–16 mm deep; hinge corner highly rounded; hinge angle 110°–120°; ribs spaced at ca. 6 per 5 mm; ribs more strongly defined at breaking edge of growth lamella, weaker following breaking edge; growth lamellae not uncommonly of two cycles, a larger cycle of 4–5 mm spaced, more prominent, raised lamellae up to 10–15 mm long, with interspersed, fine, shorter lamellae projecting 1–2 mm at <0.4 mm spacing; wide frills prominent, where preserved; transapical foramen; anterior commissure with rounded to moderate fold.

Internally, pedicle callist incompletely developed, rarely with small collar; teeth long, prominent, with weak lateral lobes, more dorsally than medially directed; minute dental nuclei apically, small dental cavities distally; dv with small cardinal pit; faintly lined cardinal process; low median dorsal septum dividing posterior part of adductor scars; hinge plate moderately thick; bulbous around inner socket ridges; low middle socket ridges; crural bases small; crura short, feathered; jugal processes curved medially, terminating in short, stubby jugal plates; dorsomedial spiralia with <11 whorls.

Remarks. This readily recognizable and quite widespread species is distinguished from *Oglupes muldea* by its larger

Fig. 26. *Oglupes visbyensis* n. sp. Statistical data compiled from specimens collected from the Upper Visby beds at various cliff localities along the N coast, early Wenlock; camera lucida drawings of medium-sized and gerontic shells.



size, strong biconvexity, more widely spaced growth lamellae and, where preserved, prominent large frills. It can be distinguished from accompanying *Gotatrypa hedei* of the Lower Visby beds by its much larger size (2-3× larger), frills, and coarse ribs. This species is widespread and distinctive, occurring in nearly all the outcrops of the Visby beds from southwest to northeast along strike, although never in great numbers. *Oglupes davidsoni* (Alexander, 1949) is a smaller, more ovoid species, lacking the wider hinge angle, and U-shaped fold of *O. visbyensis*.

Materials. Total 639 specimens. Lower to Upper Visby beds.

Buske 1, coastal cliff section ca. 3280 m NW of Västerhejde church, Lower Visby beds [11]; **Snäckgårdsbaden**, roadcut going up scarp, uppermost Upper Visby beds [SW4, 18]; **Lickershamn 1**, collections below bentonite bed (Laufeld marker 1974) [57]; **Ireviken**, Lower Visby beds, Br131339 [1 vv]; **Ireviken 2**, shoreline outcrops at base of bluffs on SW side of bay, below Höglint beds [SW6: 5]; **Gnåsvärd 1**, lowermost Upper Visby beds [SW8c: 7, and 4 uncatalogued specimens], Br103854-9 [6], Br43422 [1], Br103371 [1], Br104017-19 [3]; **Gnåsvärdshamn**, Hede collection 28, no catalog. no. [1]; **Rönklint 2**, tide level exposures in Lower Visby beds [SW43: 32], and Upper Visby beds, CK490113, Br107920-23 [4]; type locality, **Stavsklint 2**, strata about 4 m above sea level in bluffs, upper part of Lower Visby beds [SW47c: 62]; **Cementfabriken Visby**, Lower Visby beds, Br107845-47 [4], Br107850-63 [13]; **Kronvikenskanal**, Väskinde, Lower Visby beds, Br103368-71 [5]; **Gustavsvik**, udden N om Gustavsvik, Visby sn., Br107873-4 [2], Br123951-2 [2]; **Nyhamn 1**, Br105036-41 [6], Br104127-29 [3], Br105787-8 [2], Br123929 [1], Br123936-9 [4], Br134002 [1]; **Nyhamn**, Lummelunda sn., Br123940-47 [7]; **Nyrevsudd**, N om Nyrevsudd, Br43368 [1], S om Nyrevsudd Br43499, Br434501 [2]; **Visby a**, Lower Visby beds, Br42870-99 [30]; **Väskinde** sn., Lower Visby beds, Br43992-96 [5]; **Skålsö**, Väskinde sn., Br123836-47 [12]; **Norderstrand**, Lower Visby beds, Br131207 [1], Br123953

[1]; **Balsklint**, 'Stenkyrke sn., SV om Balsklint, 0-2 m ö.h.' Lower Visby beds, Br123947-50 [4]; **Brunsbö**, 'strandhäll N om Brunsbö', Väskinde sn., Lower Visby beds, Br123930-5 [4]; **Visby Hamn**, '18 fots djup vid muddring', Lower Visby beds, Br43376 [1]; **Snäckgårdet**, no catalogue number [1]; **Hallshuk**, Hal sn., Upper Visby beds, Br46571-3 [3]; **Alstädefiskläge**, Stenkyrke sn., Upper Visby beds [1]; **Kneippbyn 3**, 'strandklinten N om Kneippbyn 1', Upper Visby beds, inter-reefal parts, coastal cliffs [SW7: 207]; **Blåhäll**, Tofta sn., Upper Visby beds, Br43369-71 [3]; Locality?, Br103889-910 [22], Br103956-70 [14], Br103972-80 [9]; **Sicklings**, Klinte sn., 800 m SV om Sicklings, Br100801 [1]; **Valbytte 1**, Västergarn sn., '1600 m S om kyrkan' CJ 291655, Slite beds, Br107955-59 [5]; **Ireviken 5**, Lower Visby beds [SW81: 11]; **Nyhamn 4**, at Nyhamn, lower beach locality, Lower Visby beds, 2 km SW of Lummelunda [SW59: 39]. This species is also common in Estonia (see Rubel, 1970).

Oglupes davidsoni Alexander, 1949
Pl. 11B, figs. a-s; Figs. 28-30

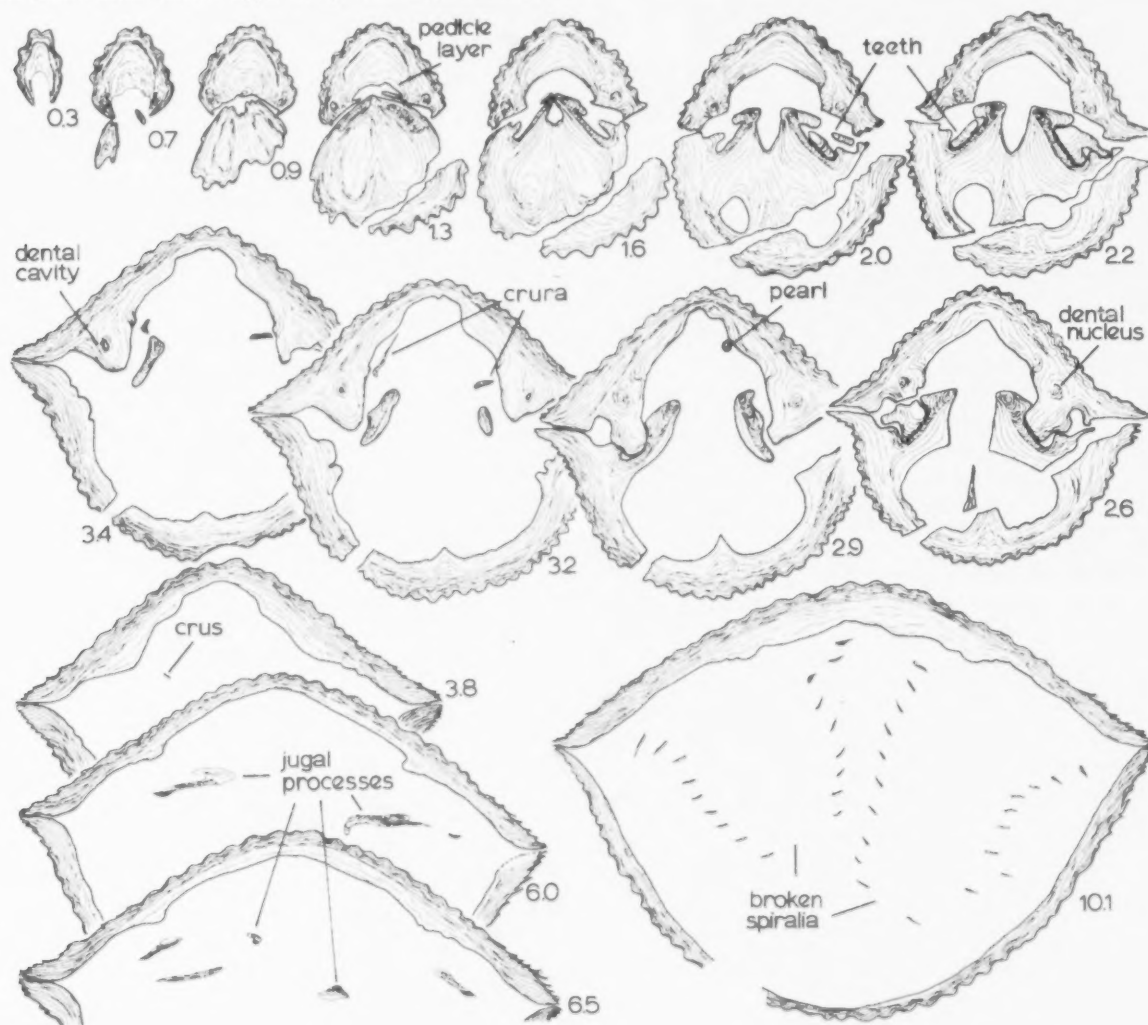
1949 *Atrypa reticularis* var. *davidsoni* Alexander 1949, p. 217.

?1978 *Atrypa alba* Lamont, p. 301, pl. 32, fig. 5.

?1990 *Atrypa torquata* Havlíček, p. 159, pl. 68, figs. 6-8.

Type locality and stratum. '... top of the Llandovery and the Woolhope Limestone; Storridge, near Malvern, Worcestershire ...' (Alexander, 1949); the holotype (A11620), and only specimen, from the locality in the Alexander collections, is from the Woolhope Limestone, which is approximately in the *riccartonensis* Zone, lower to middle Sheinwoodian, Wenlock. The Llandovery occurrence of Alexander is probably referable to *Oglupes visbyensis*. Only one other British locality, 'Stumpwood', is apparently known. On Gotland, this species appears to be confined to the upper Slite Formation (units F or G) in its western deeper distal shelf facies

Fig. 27. *Oglupes visbyensis* n. sp. Serial sections of adult shell with post-mortem damage, fracture of spiralia and dv; N.B. thick pedicle callist, dental nuclei, Upper Visby beds, early Wenlock, $\times 4$.



development, where it is locally abundant in shales 8–10 m below the resistant weathering limestones at Lerberget 4 on the island of Stora Karlsö. It is also common around Västergarn. The Gotland occurrence is within the *ellesae-lundgreni* zones. A single specimen has been found in the lower Slite beds on Fårö. Thus the species has a fairly long range from the *riccartonensis* through *lundgreni* zones.

Diagnosis. Relatively small, globose shells averaging 14 mm wide, about as wide as long. Ribs coarse, 3–4 per 5 mm, growth lamellae short, rarely more than 3 mm; anterior commissure with U-shaped fold.

Description. Small, rounded to shield-shaped, dorsibiconvex shells, averaging 14 mm wide (maximum width 21 mm), average depth 8 mm, about as wide as long; apical angle 130° – 150° , larger angle in forms which have short frills; beak small, narrow, protruding slightly; hyperclinal area in adult stages, orthocline-adpressed in neanic stages, with apical foramen commonly penetrating umbo; minute, separated del-

tidial plates in neanic shells, but small pedicle collar and no deltidial plates in adult stages. Ribs usually spaced at 3, less commonly 4 per 5 mm; growth lamellae closely, evenly spaced at less than 1 mm, ragged edged at commissure; short frills relatively rarely preserved but less than 3 mm where present, forming an extended hinge and wrapping around U-shaped, high, narrow anterior fold. Internally, thick pedicle callist commonly forming minute, pointed collar; small dental cavities apically, disappearing anteriorly; teeth long, nearly vertical with almost no lateral lobes. Socket plates thin, supported by strong hinge pad, sub-vertically oriented; notothyrial pit squared, without cardinal process. Crural bases tiny, extending ventrally and curving in an arch laterally to meet thick, short jugal processes and spiralia. Jugal processes terminating in small plates curved inwards; spiralia with 8–9 whorls.

Remarks. This species is relatively easily recognizable in the western shaly facies of the Slite beds in a belt stretching from near Västergarn to the coastal bluff at Lerberget on

Fig. 28. *Oglupes davidsoni* (Alexander, 1949). Scatter diagrams, frequency curves compiled from specimens at Lerberget 1, Lekarve 1, and Valbytte 6, Slite beds, mid-Wenlock. Camera lucida drawings of immature and mature specimens (latter showing pedicle collar).

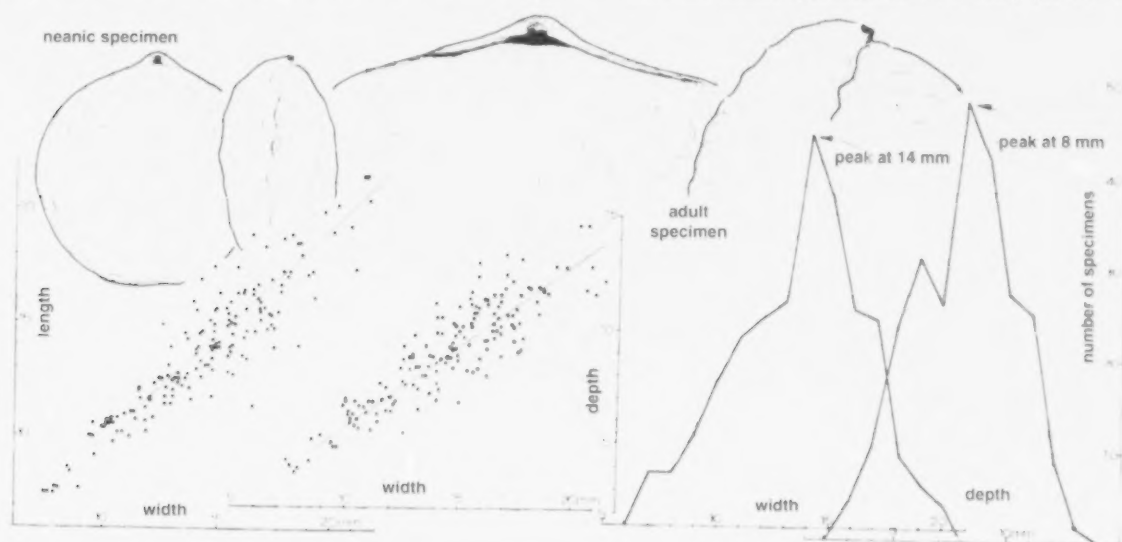
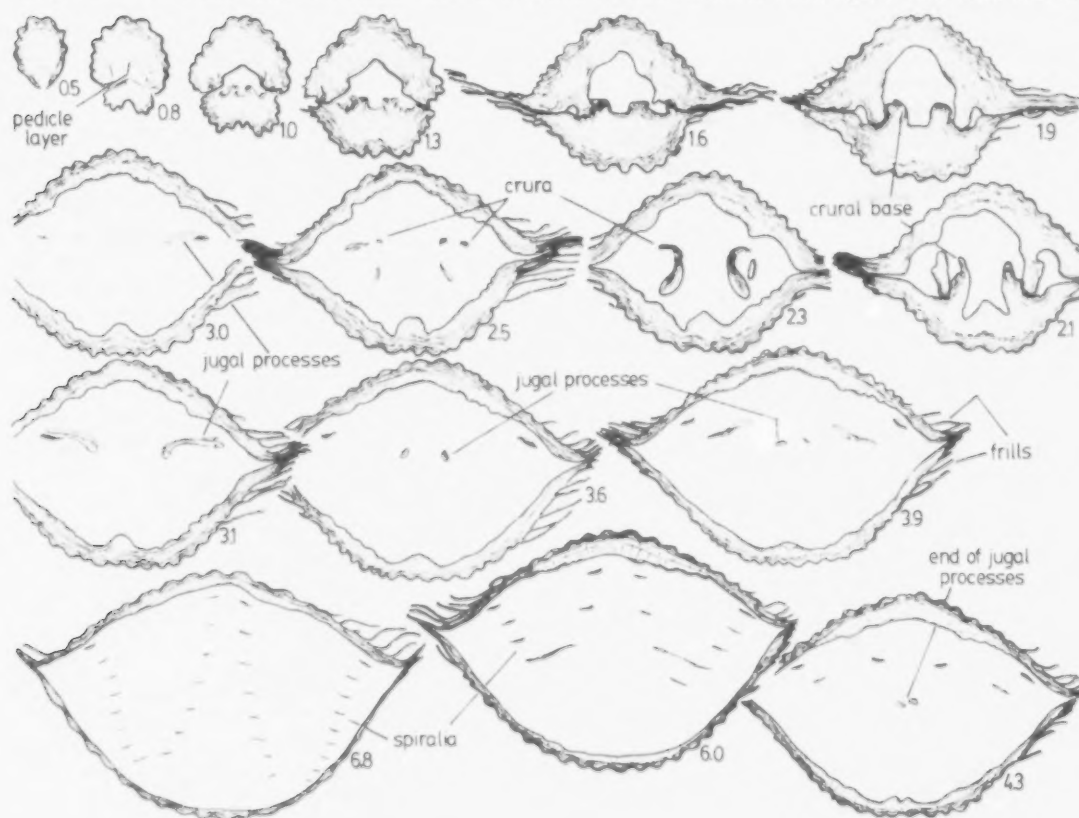


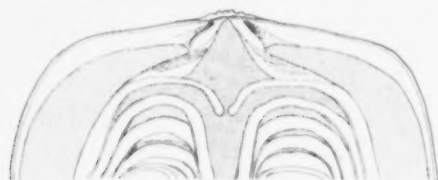
Fig. 29. *Oglupes davidsoni* (Alexander, 1949). Serial sections of typical specimen Br103940, Lerberget 1, Slite beds, mid-Wenlock. $\times 4$.



Sora Karlsö. It occurs only rarely in the centre and north-east facies of the Slite beds, where it is largely replaced by *Atrypa slitea* in muddy facies. *Oglupes davidsoni* appears to denote a deeper water, distal shelf community on Gotland,

adjacent to, and stratigraphically below, the biostromal units with *Plectatrypa* and *Septatrypa* on Sora Karlsö. Its richest development on Sora Karlsö is 3–4 m below the biostromal beds, therefore probably within units F or G of the Slite For-

Fig. 30. *Oglupes davidsoni* (Alexander, 1949). Reconstruction of internal structure, based on Br103940 from Lerberget 1, Slite beds, mid-Wenlock, $\times 4$.



mation (sensu Laufeld and Jeppsson, 1976). Its coarse ribs and small size easily distinguish it from the Mulde atrypid *Oglupes muldea*, and the coarse ribs from the Visby species *Gotatrypa hedei*. Lamont (1978) figured, but did not formally describe, a single dorsal valve from 'the silty limestone band at Gutterford Burn' (Scotland) as *Atrypa alba*, probably of late Llandovery age. It has coarse ribs like *O. davidsoni*, but is otherwise not identifiable until properly described, best remaining a nomen nudum. *Atrypa torquata* Havlíček (1990) is similar in size, convexity, and rib structure to the British species, and is probably a synonym of *Oglupes davidsoni*.

Materials. 417 specimens. **Storridge**, near Malvern, Woolhope Limestone A11620 [holotype]; **Stumpwood**, Britain, Wenlock Shale, A38497-505 [9]. Munthe et al. (1927a) referred this species in the western Slite facies to *Atrypa reticularis*. **Lerberget 1**, Stora Karlsö west coast, Br103887-954 [66], Br103974-5 [2], Br103981-104005 [25], Br106533-34 [2]; **Lerberget 4**, shales at coastal bluff N of slumped cliff, 53470:29800 [SW111: 46]; **Valbytte 6**, S of Västergarn, ditch on E side road, about 200 m S of Lekarve [SW14: 88]; **Lekarve 1**, soft-weathering shales S of Västergarn, E side road to Klintehamn, 500 m S of Lekarve [SW13, 71]; **Valbytte 7**, 100 m S of Västergarn 1, along east side road to Klintehamn [SW15, 53]; **Ramroir 1**, W coast Stora Karlsö, 300 m N of Stornasen [SW109: 13]; **Ramroir 2**, Stora Karlsö [SW110: 68]; **Lushälet 1**, 80 m N of Lerberget 4, beach, Stora Karlsö [SW112: 24]; **Lansa**, Färö, low Slite beds, Br42554 [1]; **Solklint**, low-middle Slite beds, Br105864-65 [2].

Oglupes muldea n. sp.

Pl. 13, figs. a–z, aa–ac; Figs. 31, 32

Type locality and stratum. Coastal section of low bluffs, about 300 m SW of the end of the road, **Blåhäll 1**, CJ 29050 56160, ca. 2940 m SW of Fröjel church [= SW16: see Calner et al., 2000]. Soft-weathering grey calcareous shales at the base of a 3 m thick section, from the upper Mulde Fm., associated with other brachiopods (esp. *Leptaena*), and small finger-shaped heliolitids, solitary rugosans, small favositids. At Mulde Tegelbruk 2 (Mulde Brick Clay Member), from which most specimens were collected, corals are absent, but bryozoans are common encrusters, and associated fauna includes large *Meristina*, *Leptaena*, *Visbyella*. On Gotland this species is only derived from the Mulde Marls, probably equivalent to the *nassa* Zone, middle Homeric. In England the same species occurs in the Farley Member [= Tickwood beds], upper Coalbrookdale Fm., Homeric, late Wenlock.

The name of the species is taken from the Mulde Tile Quarry in which this is the only occurring atrypid species.

Diagnosis. Medium sized, averaging 19–23 mm wide, 18–20 mm long, 11–14 mm deep; moderately biconvex to weakly dorsibiconvex, wider than long shells, rounded outline, nearly straight shoulder lines; very closely spaced, fine ribs at 6 per 5 mm; short growth lamellae; weak anterior fold.

Description. Shells rounded in outline with weak shield shape towards hinge, biconvex to weakly dorsibiconvex, not globose; vv slightly inflated posteriorly, but gently convex anteriorly; wider than long, medium sized, widths 19–23 mm, lengths 18–20 mm, depths 11–14 mm for adult sizes (cumulative curve for shell depth shows two peaks, one at 4 mm and another at 12 mm); hinge angles wide, 140° – 150° ; shoulder line nearly straight, weakly indented; hinge corners rounded; ribs reticulate, strong in the centre of the shell, fading towards hinge corners, from 5–7 ribs per 5 mm (average 6); relatively strong mid-rib pair or double pair on ventral umbo, making the shell weakly carinate in very early growth stages, with matching groove on dv; growth lamellae closely spaced, numerous, at 1–1.5 mm; weak wave-like trends intersecting ribs at each growth lamella, projecting 1–2 mm; growth lamellae crowded at anterior commissure; shells normally not preserving distinct frills, only broken remnants; vv growth lamellae flexed away from shell; anterior commissure weakly concave in adult shells; beak small, pointed; area hypercline in adult stages, leaving small gap above dorsal umbo; foramen transapical, minute, or absent (covered by incurvature of beak); neanic growth stages with erect beak, small orthocline area; small, triangular deltidial plates or pierced apical foramen; small pedicle collar visible in some adult specimens.

Internally, shell wall moderately thick, especially posteriorly; pedicle callist well developed into platform, some with collar; muscle scars in adults strongly incised; ventral diductors large, nearly half shell length, striated, subdivided into two regions; central adductors heart shaped; dorsal adductors rounded, bilobate; weak vascular canals and strong pits; teeth with minute dental nuclei, no cavities, of median length, medio-dorsally directed, with well-developed lateral lobes; dv with thick, solid hinge plate apically, small, comb-like cardinal process lining cardinal pit, inner socket ridges; socket plates with prominent inner socket ridges supported by bulbous hinge pad, middle socket ridges large; median septum strong; crural bases rounded, leading to fibrous, feathered crura; jugal processes delicate, curved, nodose at their ends; very small terminal jugal plates; spiralia dorsally directed, 10–11 whorls.

Remarks. This is one of the most abundantly represented atrypids in the Gotland collections: it has usually been assigned to *Atrypa reticularis*. This is the youngest species of *Oglupes* known from Gotland. The moderately biconvex to dorsibiconvex shell lacks the strong ventral inflation seen in other *Oglupes* from Gotland, and the vv may have relatively weak convexity, which, with the short frill, may give the shell the appearance of grading towards *Atrypa*. This is the most abundant, and commonly the only atrypid in much of the Mulde beds, but for rare *Plectatrypa* and locally abundant *Glassia*. It also occurs in the upper Coalbrookdale Formation (Tickwood beds) of Britain. The species is distinguished from *Oglupes visbyensis* by its weaker ventral con-

Fig. 31. *Oglupes muldea* n. sp. Statistical variation compiled from Blåhäll 1, Djupvik 1, Mulde Tegelbruk 2, mid- to late Wenlock, Mulde Marl localities, with camera lucida drawings of medium and large shells.

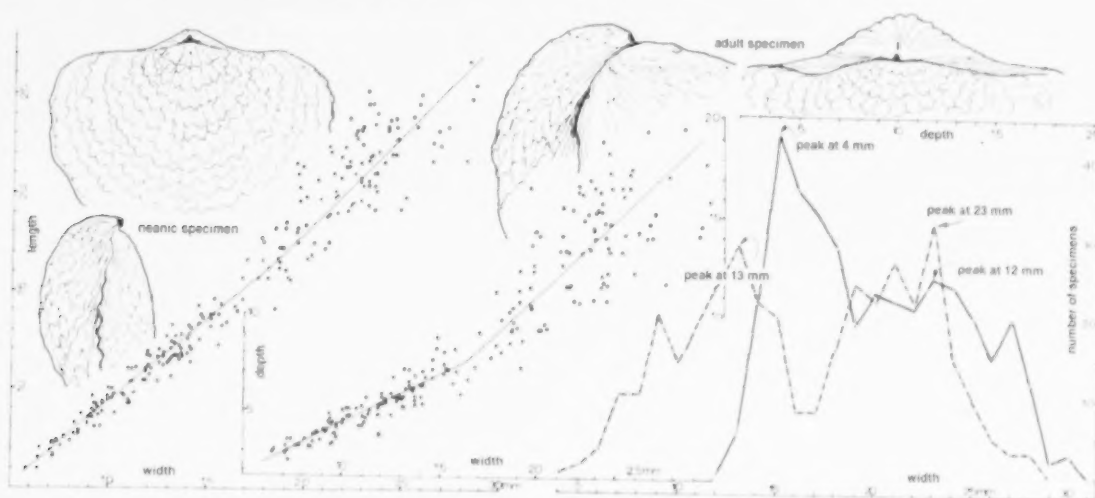
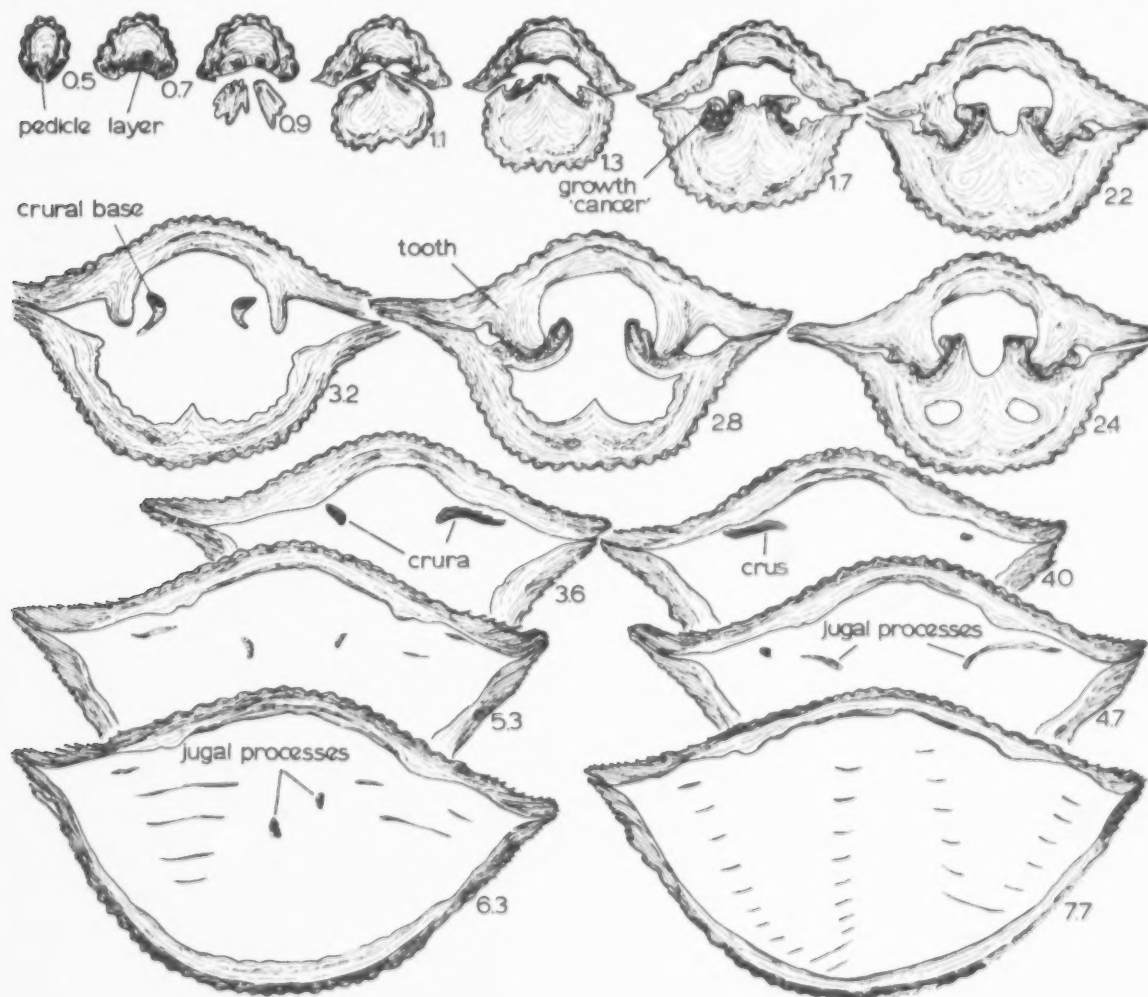


Fig. 32. *Oglupes muldea* n. sp. Serial sections of adult shell, Blåhäll 1, Mulde Marl, mid- to late Wenlock: note deceptive appearance of 'septalium' due to angle of sectioning, $\times 4$.



vexity, lack of strong, wide frills, more incised ribs, and wide shell with weak fold. It is much larger and more finely ribbed than *Oglupes davidsoni*, which precedes it in the Gotland succession.

Materials. Total 407 specimens from the Mulde Marl in SW Gotland and upper Coalbrookdale Formation (Tickwood beds) in Britain. This species is very well preserved at nearly all the localities of the Mulde Marl. **Blåhäll 1**, type locality, coastal bluffs [SW16: 126]; **Mulde Tegelbruk 1**, Fröjel sn., CJ 3127 6048, ca. 2080 m NNE of Fröjel church, type locality Mulde Marl, Br10572-98 [39], Br105069-71 [3]; **'Mulde Märgelstein'** (probably Mulde Tegelbruk), A46102-24 [23]; **Sicklings**, 600 m SW om Sicklings, Klinte sn., Br107999-8000 [stated to be Slite but probably Mulde Marl: 2]; **Djupvik 1** [or Djauvik on maps], Eksta sn., lower Mulde Marl, Br42473-74 [2], Br42476-86 [11], Br104006-8 [3], [SW88: 105]; **Mulde Tegelbruk 2**, excavations for crayfish ponds on west side of highway, 700 m N of stone boat [SW96: 173]. Railway cutting **Farley Dingle**, at Tickwood ('Tickwood' beds, Coalbrookdale Fm., Farley Mbr., or 'Wenlock Shale'), B34764 [11], B34766 [15], from Walker collection 1909 (this outcrop is no longer accessible, but was known to Davidson, also providing the types of *Glossia elongata*).

Endrea Copper, 1996b

Type species. *Endrea echoica* Copper 1996b, reefal lower Slite beds, Sheinwoodian, early Wenlock, Gotland.

Range and distribution. Wenlock–Ludlow, Gotland, Estonia, Britain.

Diagnosis. Medium to large, biconvex–dorsibiconvex, shield-shaped; small orthocline–anacline area; apical foramen surrounding small deltidial plates even in adult shells; highly arched, tubular–imbricate ribs, short frills or growth lamellae; fine concentric filose micro-ornament; commissure weakly to strongly folded; pedicle callist very thin to lacking; teeth with small to medium dental cavities; jugal processes terminating in small, weakly curved jugal plates; spiralia with fewer than 10 whorls.

Remarks. The most striking feature, seen only in well-preserved material (in all species identified), is the fine micro-ornament intersecting the ribs and the tubular nature of the ribs, with growth lamellae projecting as short frills which almost look like short spines where broken. Early growth stages, with a proportionally large orthocline area, and tubular ribs may suggest affinities with *Spirigerina* instead of *Atrypa*. However, the abundant overlapping growth lamellae and presence of short growth lamellae, and internal structure of the hinge plates, suggest relationships lie with the *Atrypinae*. The genus is distinguished from *Atrypa* by its tubular–imbricate ribs, very short frills or no frills, filose micro-ornament (where preserved), small deltidial plates, dental cavities, and lack of a pedicle callist. *Rugosatrype* is most similar, but has finer, more *Atrypa*-like, flatter ribs, and a convexoplane shell. In its ribs *Endrea* begins to mimic the genus *Spinatrypina* Rzhonsnitskaya 1964, generally aligned in the subfamily *Spinatrypininae*, but it differs in its lack of rib imbrication and in possessing short, flat frills, and relatively small dental cavities. One species, *Endrea tubulosa* (Bassett

and Cocks, 1974) was previously identified as *Spinatrypina*. It is distinct from relatively flat-shelled *Limbatriypa* Copper 1983 in possessing abundant growth lamellae which hug the shell surface instead of lamellae which jut out perpendicular to the shell, and in its coarser ribs and biconvexity. The relationship to the genus *Atrypinella* Khodalevich 1939 and *Reticulatrypina* Savage 1970 (see also Havlíček, 1991, p. 163) is not clear. Both of these genera tend to be extremely finely ribbed, very small in size, and generally tend to have a ventral keel. There are similarities in disposition of the delthyrium and convexity, but large specimens of *Endrea* are more *Atrypa*-like in general shell shape.

The ancestry of *Endrea* is problematic: it shares affinities with *Protatrypina* from which it may have been neotenuously derived by retaining its deltidial plates and orthocline beak in adult specimens (although some large shells have a large expanded foramen, losing their deltidial plates). However, *Protatrypina* has an *Atrypa*-like rib structure consisting of wavy low ribs, and lacks growth lamellae and frills. There is a size increase in *Endrea* from its lowest occurrence in the Axelro reefal facies of the Upper Visby beds (earliest Wenlock) to species in the Slite beds and the Ludlow Eke beds. All the species are generally associated with small patch reefs or with coral, bryozoan, and stromatoporoid biostromes, and calcareous sandy substrates, suggesting attachment in thickets constructed by those coralline elements, and higher energy regimes.

Species tentatively assigned.

Limbatriypa branzovensis Havlíček 1990, Prague Basin, upper Motol Fm., late Wenlock.

Endrea echoica Copper 1996b, Gotland, lower Slite beds, early Wenlock.

Endrea ekenia n. sp. Gotland, Eke beds, middle Ludlow.

Atrypa reticularis var. *lonsdalei* Alexander 1949, Dudley, Much Wenlock Limestone, late Wenlock.

Spinatrypina tubulosa Bassett and Cocks 1974, Likershamn, Gotland, Upper Visby beds, early Wenlock.

Endrea echoica Copper, 1996b

Pl. 14, figs. a–k; Figs. 33, 34

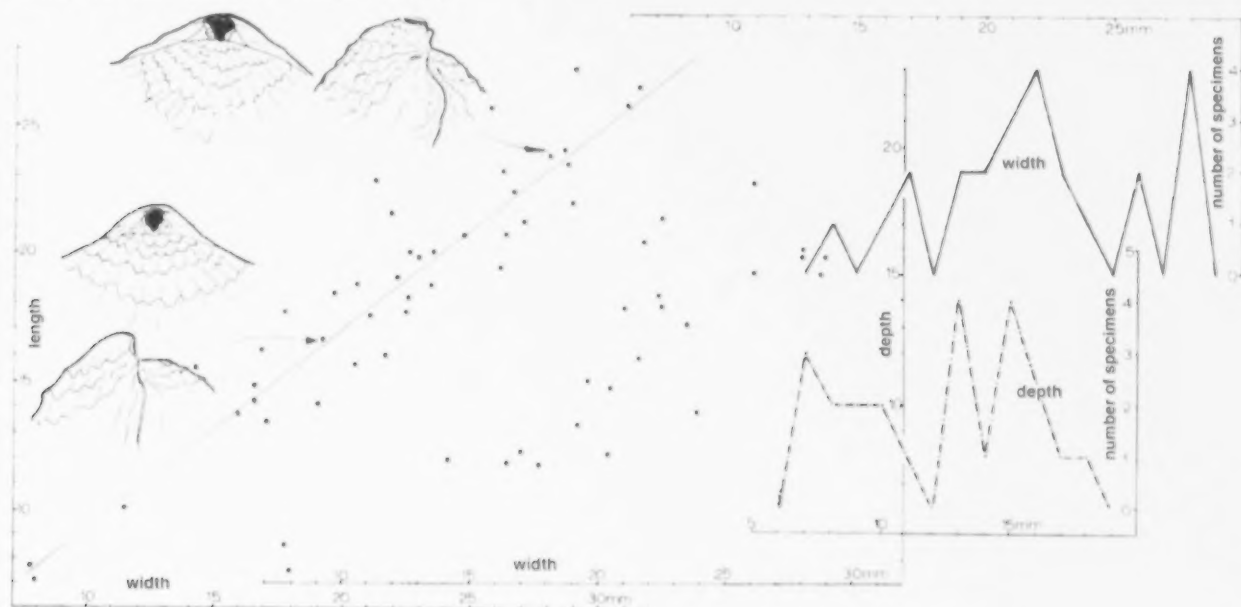
1927 *Atrypa reticularis* forma *concentrica* Hede, in Munthe, Hede, and Lundqvist, p. 21.

1970 *Atrypa dzwinogrodensis* Kozłowski 1929; sensu Rubel, pl. 19, figs. 1–12.

1996b *Endrea echoica* Copper, p. 919–920, fig. 4.

Type locality and stratum. **Stutsviken 2**, low beach outcrops, ca. 100 m W of fishing huts, northwest coast of Fårö island; map sheet 7J Fårösund SO 26520:92870 [locality SW106]; the species is found most abundantly in the second set of small coral patch reefs and flank beds on the west side of the bay, about 100 m N of the inshore end. It occurs with abundant branching tabulates, branching bryozoans, cystiphyllid phaceloid and cerioid–aphroid rugosans, and common *Xanthea lamellosa* (although *Xanthea* is more common in the southern set of reefs on the inner shore) and *Stegerhynchus* sp. The species was found both on the reef flanks and cores. The host sediment is a yellowish to grey–brown bindstone–bafflestone with a matrix that is largely calcarenitic, assignable to the lowermost Slite beds, unit 'A' of Hede (1960), or

Fig. 33. *Endrea echoica* Copper, 1996b. Statistical variability compiled from all localities available, but primarily the type locality at Stutsviken 1, 2, 3; middle Wenlock; specimen numbers inadequate to produce consistent curves for this large shell. Camera lucida drawings of beak detail, two specimens indicated.



possibly the Högklint beds equivalent. In the older literature, and in collections, this locality is in the same area as 'Lansa', and the most abundant museum collections of this species bear that label. The species was not discovered in the larger patch reefs exposed about 1.3 km further to the NW at Hällagrund. The stratigraphic level of the species is approximately within the *linnarsoni* graptolite Zone, middle-upper Sheinwoodian, Wenlockian.

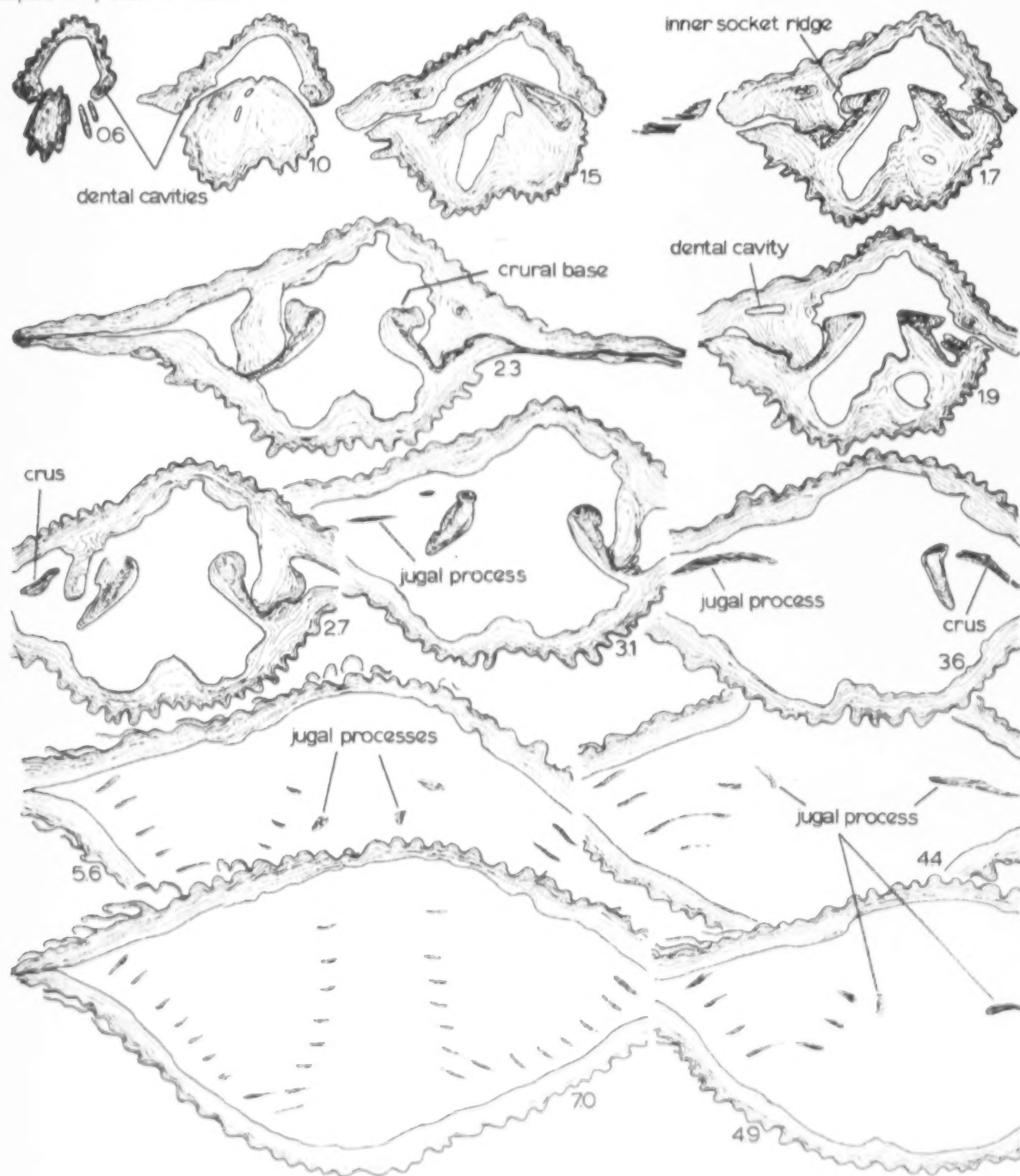
Diagnosis. Relatively large and wide (gerontic shells to 31 mm width), straight-hinged shells with inflated dorsal valve; widely overlapping growth lamellae along the anterior commissure, marked by a strong dorsal fold.

Description. Wide, globose, dorsibiconvex, shield-shaped shells, about 15–20% wider than long, averaging adult widths 21–28 mm, averaging 13–16 mm deep; long, rather straight hinge interrupted by overlapping beak to produce hinge indentation, maximum width near hinge, rounded hinge corners, with overall outline almost semicircular. Ventral valve more convex apically but tending to flatten anteriorly in large shells; dv strongly convex, broadly rounded; anterior commissure with high U-shaped fold. Ventral beak jutting out, orthocline area; prominent pedicle foramen flanked by two large deltidial plates; with lip around foramen margin. Ribs sharp, clear, nearly tubular, relatively fine apically but expanding slightly distally towards the shell margins, with 5–7 ribs per 5 mm towards the mid-shell area and anterior commissure, and ca. 7–8 ribs per 5 mm apically; ribs interrupted by distinctive growth lamellae every 2–4 mm, regularly spaced, overlapping towards the shell margins to give shell short fringe around commissure; fringe probably adding 3–5 mm to total shell width beyond body cavity; well-preserved shells show numerous fine micro-growth lines. Internally,

lacking pedicle callist; deltidial plates shunted off towards the sides of the pedicle cavity; dental cavities distinct apically, but slit-like anteriorly; teeth strong, widely spaced, pointing anteriorly, long, prominent, lacking distinct lateral lobes, dv with relatively modest hinge plates, thin socket plates strengthened by reinforcing hinge pads, clear middle socket ridges; cardinal pit narrow, exposing long median septum; inner socket ridges relatively thin, horizontal initially, then becoming more bulbous distally, expanding into small, rounded crural bases. Crura bent at right angles to socket plates, flexed laterally to curve around teeth; jugal processes long, thin, fairly wide apart, curved around crook-like medially and terminating in small jugal plates pointing dorsally; spiralia, maximum <10 whorls.

Remarks. It is not certain if Hede (in Munthe, Hede, and Lundqvist, 1927) actually identified this species from the Högklint Limestone, as specimens with the identification 'forma *concentrica*' cited by Hede were not discovered in the Riksmuseet collections. The name *concentrica* might well have come from the distinctive, fine micro-ornament of concentric filae. The material herein derives from the lowermost part of the Slite beds (unit A), primarily from Fårö, although fragmentary material in the Högklint could be conspecific and is broadly concentric in form. This species is distinguished from *E. tubulosa* (Bassett and Cocks, 1974) in its much larger (2–3× larger), globose, dorsibiconvex shell, and plicate commissure: it is similar in having tubular ribs with the same micro-ornament, especially in early growth stages, but also evident in well-preserved adult shells. It has been mistaken for a species of *Atrypa*, which is similar in size, but *Atrypa* has no concentric filae, nor apical foramen, nor deltidial plates, and differs internally in its thick pedicle callist and solid teeth.

Fig. 34. *Endrea echoica* Copper, 1996b. Serial sections of paratype Br103884, 'Endre, dike vid landsvägen till Endre, ca. 1250 m fra Österport, Visby', middle Wenlock, $\times 5$.



The species appears to be a typical coral patch reef and peri-reefal dweller in the lower Slite beds around Stutsviken, in which Munthe et al. (1936) identified it as *Atrypa reticularis*. It is found sporadically in the outcrops of lowermost Slite beds from Fårö to west of Visby, usually as local concentrations only.

Materials. Total 105 specimens. **Stutsviken 2** [type locality], set of coral patch reefs and flank beds, about 50 m N of Stutsviken 1, 71 Fårösund [SW106: 15]; **Stutsviken 3**, set of small coral bioherms on the inshore end of the bay, ca. 100 m W of Stutsviken 2 [SW107: 14]; **Lansa**, Fårö sn. [this is probably very close to the type locality Stutsviken 2].

Br123954-57 [4], Br42535-58 [24], Br43402-4 [3], Br43397-401 [5], Br43670-4 [5]; Munthe et al. (1936) identify this form also from '350 S om Marpis', near Noistur, and Lautur on Färö island. **Fiskestuga, Stutsviken 1** [Bassett colln: 9051G57-73:17], loose material from beach ridges, 50 m W of Fiskestuga in SE corner of Stutsviken; **Fiskestuga Stutsviken** [= Stutsviken 1?], loose shells 50 m NW of Fiskestuga, 90-51G-555-7 3 [19]; **Endre**, 'dike vid landsvägen till Endre, ca. 1250 m fra Österport', Visby, Br103862-66 [5]; Br103878-86 [7]; **Stenkumla**, '750 m N om Martille, vid landsvägen', Br107900 [1], Br107894-6 [4], Br107913-5 [3], Br107916-8 [3], Br107907 [1], Br107910-12 [3]; **Kärningen 1**, Visby, Br124079 [1]; **Blase**, 'kanal N om Blase', Fleringe sn., Br124085-87 [6], Br124101 [1]; **Stora Myre 1**, Martebo sn., Br1291211-4 [4], Br104106 [1]. The species thus occurs as far NE on Färö as the extent of Slite strata and on Gotland, to near Visby and SW of Visby.

Endrea tubulosa (Bassett and Cocks, 1974)

Pl. 15A, figs. a-g; Fig. 35

1974 *Spinatrypina tubulosa* Bassett and Cocks, p. 29-30, pl. 8, figs. 3-6.

1990 *Spinatrypina tubulosa*, Bassett p. 250, fig. 6B.

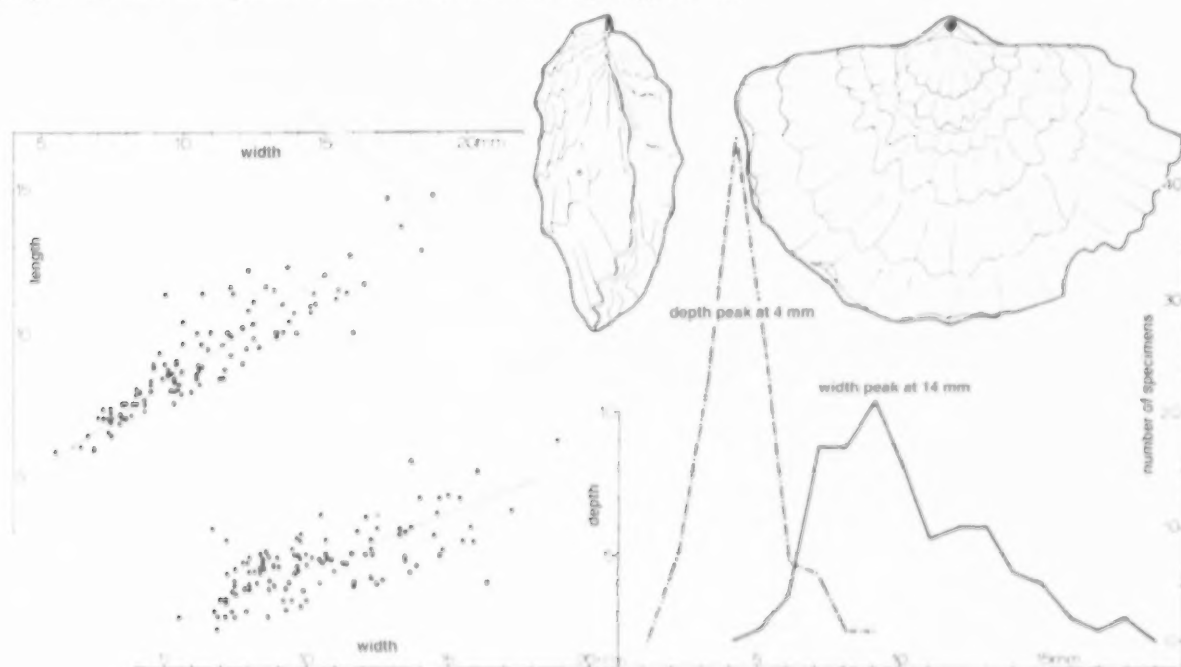
Type locality and stratum. The type specimens from the Lindström collection are labeled 'Lickershamn', 7J Färösund SV, NV, 5192:1262, 'ca. 4.35 km NNW of Stenkyrka church' (Laufeld, 1974, p. 92), with probable derivation from the Upper Visby beds, Rövar Lilja Mbr. Specimens collected personally were common only in and around the smaller patch reef

horizons of the Upper Visby beds, which mark some localities on the north coast. The type locality allocated by Bassett and Cocks (1974) is Lickershamn. The species also appears to be common in the lower part of the Högklint Fm., probably unit A, or the Korpklint Member. The species thus ranges approximately through the *murchisoni* and *riccartonensis* zones, i.e., middle Sheinwoodian, early Wenlock. It can locally be one of the most abundant atrypids in the perireefal and reefal Axelro facies of the Upper Visby Fm., and is commonly accompanied by *Xanthea scabiosa*.

Diagnosis. See Bassett and Cocks (1974). Shells small (average width 14 mm), relatively flat and thin (average depth 4 mm), lacking dorsal fold, with long relatively growth lamellae, straight hinge, narrow protruding beak.

Description. Relatively small to medium sized (maximum width 18 mm, width average 14 mm), wider than long, width less than 3× depth, weakly biconvex, relatively flat shell; shell depth peak at 4 mm (thickest shell 7 mm); small, protruding beak; distinct orthocone to weakly anacoline area; minute apical foramen; small triangular deltidial plates; hinge line relatively long, strongly indented near beak; hinge corners at 80°-90°, subangular rounded; anterior commissure rectimarginate, lacking fold. Ribs medium, 3-4 per 5 mm, subtubular, relatively high crested, deep troughed; growth lamellae 4-6 mm long, overlapping at anterior commissure, flaring at rib crests, producing short frills; ribs and troughs marked by micro-ornament of numerous, very fine, distinct concentric filae. Thin, fragile shell wall, small hollow deltidial plates, distinct dental cavities, thin hinge plates. Internal shell structure not sectioned.

Fig. 35. *Endrea tubulosa* (Bassett and Cocks, 1974). Statistical evaluation of specimens from Lickershamn type locality, early Wenlock; depth peak at 4 mm, width peak at 14 mm. Camera lucida drawing of typical shell.



Remarks. Bassett and Cocks (1974) assigned this very distinctive and readily identifiable species to *Spinatrypa*, a common Devonian genus, presumably on the basis of similarity in the tubular-imbriate nature of the ribs. However, this species appears to be ancestral to a much bigger shell, *Endrea echoica*, that occurs in the overlying Slite beds. *E. echoica* is almost identical in its early growth stages to *E. tubulosa*, but varies considerably in adult stages by becoming large, highly convex and developing strong beak incurvature. This matches the increase in size seen from the Upper Visby strata into lower Slite of a co-occurring atrypid genus *Xanthea scabiosa* to *X. lamellosa* (Lindström, 1861).

Materials. 72 specimens. *Upper Visby beds*: Rövar Lilja Mbr., type locality, **Lickershamn**, Br43186-222 [27], Br115495-526 [32], Br110941 [1]; **Stuguklint** (? = Stuklint, ca. 1 km NW of Lickershamn), 'fr. ett litet rev.', Br107944-5 [2]; **Körpklint**, Västerhejde, 'fr. mägelfickorna i reven', Br103426-33 [8]; **Visby**, Br110998 [1]. *Lower Högkint Fm. (Körpklint Mbr.)*: **Ringvide**, 'nedfartsvägen till stranden' [this is on the S outskirts of Lickershamn], Br103458 [1].

Endrea lonsdalei (Alexander, 1949)

Pl. 16A, figs. a-t; Figs. 36, 37

?1839 *Atrypa aspera* Schlotheim 1813, Sowerby, pl. 12, fig. 5.
1949 *Atrypa reticularis* var. *lonsdalei* Alexander, p. 214-215, pl. 9, figs. 3a-d.

?1978 *Atrypa* sp., Hamblin et al., fig. 3.

Type locality and stratum. 'Wenlock Limestone of the Dudley area . . . Dudley Castle Hill, Dudley', Staffordshire (Alexander, 1949, p. 214). This level of the Dudley [= Much Wenlock] Limestone is Homerian, late Wenlock, probably in the *nassa* Zone. Corfield et al. (1992) suggested the whole of the 'Much Wenlock Limestone' in the West Midlands, in-

cluding the intervening nodular beds between the lower and upper limestones, spanned the high *lundgreni* through *ludensis* zones. The Dudley Limestone is from 46 to 52 m thick: the exact horizon from which Alexander's specimens were collected is unknown, but probably these come from the lower levels of limestones (or the Nodular beds) and are therefore of late, but not latest, Wenlock age. I personally collected specimens from the west and east side outcrops of the 'Nodular beds' (localities B and D, Wren's Nest; Hardie, 1971), thus probably within the *nassa*, or lower *ludensis* Zone. Specimens in other collections may also have come from the shales directly above the lower limestone, since Hamblin et al. (1978) mention '*Atrypa*' as occurring from the 'Lower Limestone' through the 'Passage beds', i.e., throughout the 'Dudley Limestone'. Alexander's collections were sufficient for a statistical analysis. Hurst (1975b) assigned most of the Dudley carbonates to a higher energy *Sphaerirhynchia* community, but lumped all Wenlock atrypids as *Atrypa reticularis*, probably including *E. lonsdalei* under this name, making no reference to Alexander's work. This species appears to be absent in Gotland (?Hunninge 1, questionable specimen), where it should be present from high Slite beds through Klinteberg facies: appropriate calcimicrobial mound or nodular limestone facies appear to be missing.

Diagnosis. Medium-sized shells, averaging ca. 14 mm wide, 7 mm deep, somewhat globose, with very short frills along the hinge axis; foramen commonly penetrating dorsal umbo.

Description. Relatively small shells, average width 13–16 mm [peak at 14 mm], length exceeding width in early growth stages, but reversed in adult shells, average depth 6–8 mm [peak at 7 mm]; vv moderately convex, dv strongly convex; umbo inflated; anterior fold U-shaped, sharply defined, commonly with upcurled edges. Distinct, small, rounded foramen; small area orthocline in most, anacline in some speci-

Fig. 36. *Endrea lonsdalei* (Alexander, 1949). Statistical summary of specimens from Dudley and Wren's Nest, late Wenlock; with width peak at 14 mm, depth at 7 mm. Camera lucida sketch of adult specimen posterior.

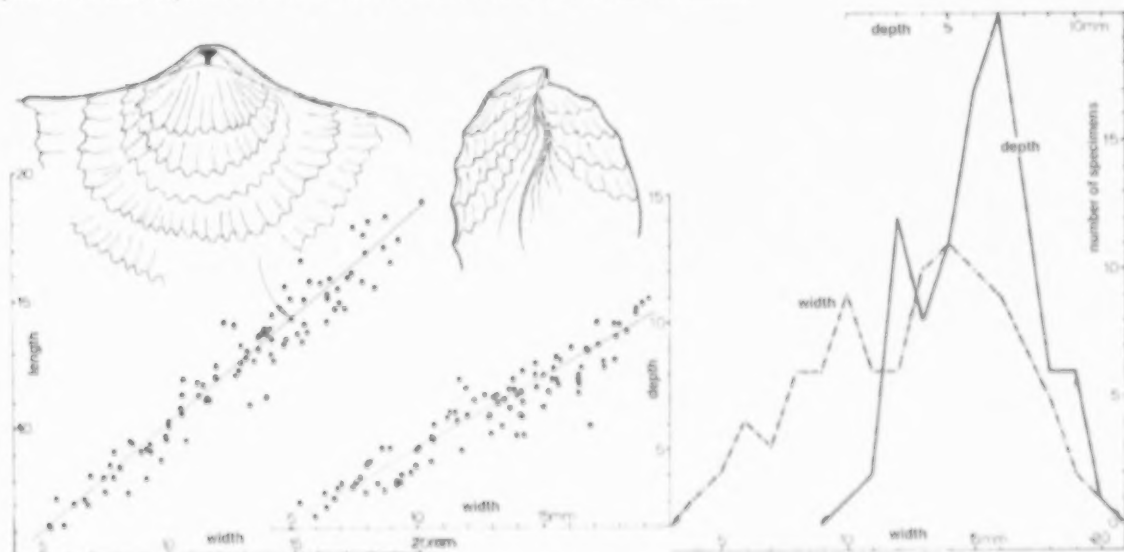
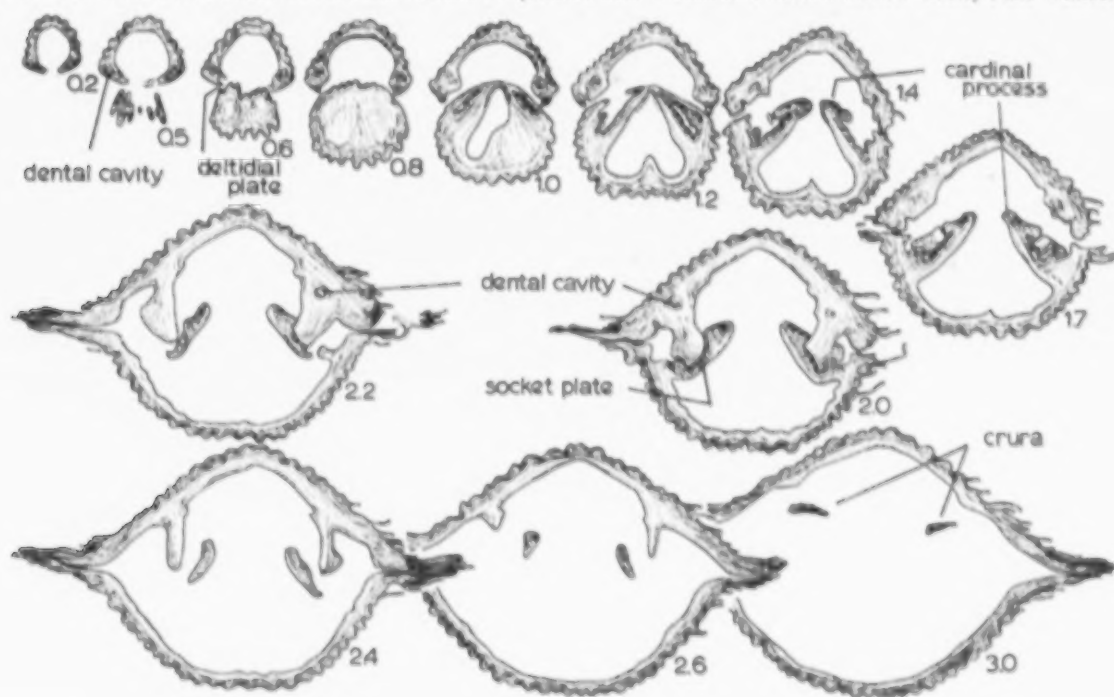


Fig. 37. *Endrea lonsdalei* (Alexander, 1949). Serial sections of specimen from Alexander collection labeled 'Dudley', late Wenlock, $\times 5$.



mens, almost hypercline in some gerontic shells, invariably orthocline in early growth stages; many adult specimens with foramen perforating umbo, reduction or loss of deltidial plates. Ribs spaced at 5 per 5 mm; frills short, evenly spaced at up to 2.0–2.4 mm, crowded anteriorly, projecting at high angle to shell; some shells showing extension of frills along hinge, providing shell with hinge elongation; micro-ornament absent in most shells, with ribs nearly smooth; some shells show concentric micro-ridges or micro-growth lines. Internally, vv thin-shelled, lacking apical pedicle callist; deltidial plates minute, hollow, flanking small prominent foramen; small oval to rounded dental cavities at apex, retained distally, opening laterally; teeth dorsally directed, relatively long, slender. Dorsal valve with weak cardinal process lining cardinal pit; wide, open socket cavities; slender hinge plates; thin hinge pads supporting fragile socket plates; crural bases slender, pointed, elongated, expanding to short, simple, slightly bushy, and fibrous crura. Spiralia and jugal processes not intersected on specimen examined, but on weathered specimen with up to 7 whorls.

Remarks. This late Wenlock shell most resembles the Ludlow Gotland species, *E. ekenia*, from which it is statistically difficult to separate in its common dimensions [the peak width and depths are the same]. The British species tends to have an obscured foramen and hypercline area, or the foramen is expanded through the umbo (Fig. 59), whereas the Gotland species appears to retain the orthocline foramen and exposed deltidial plates in adult shells. In addition, the growth lamellae tend to produce a characteristic wing on the shell corners along the hinge, not seen in the Gotland specimens. Internally, the shells are similar. *Endrea lonsdalei* has not yet

been found in equivalent age strata of Gotland (i.e., high Slite-Klinteberg levels), where the nodular or calcimicrobial mudmound facies is absent. Although average width dimensions are similar to relatively flat-shelled *Endrea tubulosa* (Bassett and Cocks, 1974), with which it shares the filose micro-ornament, the Dudley species is rounded and globose, often with a transapical foramen and tendency for the beak to be incurved and area to become hypercline in gerontic stages.

Materials. Total 488 shells, all from Britain (except 1 doubtful specimen), probably spanning the upper *lundgreni* through *ludensis* zones. 'Wenlock Limestone, **Dudley Castle Hill**' [type locality], A11622, A30320–A30324 [5], A30422–A30432 [14], A30437–A30442 [6], A30454–A30462 [9]; 'Wenlock Limestone, **Walsall**', B605 [5]; 'Wenlock Limestone, **Dudley**', B2414 [1], B606 [5], B3919 [2], A26703–A26709, A6714 [8], A26676–A26693 [14]; '**Wren's Nest**, **Dudley**', A1121–A1125, A1128–A1130, A1132–A1133, A1135 [11; Adam Sedgwick colln.]; **Nodular beds at Wren's Nest**, associated with small patch reefs of bryozoans, stromatoporoids, and corals, at base of Much Wenlock Limestone, unit GB10 (29), GB23 (149), GB33 (176; Yvonne Pocock collection from Wren's Nest). A number of small specimens from the Wenlock Limestone of Dudley may be immature *E. lonsdalei*, and are tentatively assigned there: **Dudley**, 'Wenlock Limestone', A26582–9 [8], A26595–604 [10], A26605–12 [8 + 2 unnumbered]. Shelf margin, '**Coalbrookdale**, **Benthall Edge**, Wenlock Limestone', B9876 [2]; '**near Benthall Edge**', B5455 [12]; 'Wenlock Limestone, **Wenlock Edge**', B608 [11; precise location uncertain]. Klinteberg beds, ?**Hunninge 1**, Br107925–28 [4; questionably assigned].

Endrea ekenia n. sp.
Pl. 16B, figs. a-n; Figs. 38-40

Type locality and stratum. Eke Formation, Rhizophyllum Limestone Member, open field, Lau Backar 1 [type locality], 6J Roma SV, CJ 5775 5209, [?] upper *leintwardinensis*-*kozłowski* zones, middle Ludfordian, late Ludlow. In Laufeld and Jeppsson (1976) the Rhizophyllum Member straddles the boundary between the upper part of the *leintwardinensis* and *bohemicus* zones. The horizon of the lowermost Eke beds is defined by Cherns (1982, 1983) as of late to post-*Sactograptus leintwardinensis* age, which means that *Endrea ekenia* must be younger than this and probably within the *kozłowski* Zone. Specimens occur in about 1 m thick, surface outcrops of yellowish weathering calcareous shales and thinly bedded, winnowed calcarenites including crinoid ossicles, common cup corals, colonial rugosans, and favositids (in part almost biostromal), and the brachiopods *Microsphaeridiorhynchus*, *Isorthis*, *Homeospira*, *Delthyris*, and *Leptaena*. According to Cherns (1983), small reefs of the Eke beds are near the type locality, and some brachiopod nests occur in these small mounds. Conditions indicated are strong currents and higher energies, in shoaling calcarenite to patch reef and peri-reefal facies, but outside the proximal shelf area of oncoid accumulation (see also Samtieben et al., 2000). For lists of the fauna see Laufeld (1974b) and Cherns (1982, 1983). At Burgen 4, similar specimens indicate the species may range down into the uppermost Hemse beds, unless this is Eke Fm.

Diagnosis. Medium sized, averaging 14 mm wide, 13 mm long, 7 mm deep, strongly biconvex, globose; numerous, short overlapping frills projected away from the shell surface; small, distinct orthocline area with apical foramen, deltidial plates; spiralia of 6-8 whorls.

Description. Slightly wider than long, biconvex, generally rounded in form, hinge corners rounded enough to be ab-

sent; widths 10-15 mm (peak at 14 mm), lengths 10-14 mm (peak at 13 mm), depths 5-8 mm (peak at 7 mm). Beak protruding, pointed, somewhat triangular, apical angles high (120° - 140°); area apsacline in early growth stages but orthocline in mature shells; small, rounded apical foramen flanked by small, triangular deltidial plates with a clear lip. Ribs clearly defined, highly arched, tubular, concentrically wavy, and upturned at 1 mm spaced, very regular growth lamellae; short projecting frills of about 1-2 mm. Anterior commissure gently folded.

Ventral valve lacking apical pedicle callist, but with minute, hollow deltidial plates; distinct apical dental cavities opening distally but reduced to dental nuclei apically; teeth long, delicate, dorsomedially directed, with small lateral lobes. Dorsal valve with large cardinal pit bisected by prominent dorsal septum; hinge plate relatively thin, delicate; inner socket ridges prominent, but not inflated; crural bases small; crura laterally deflected, solid, thin; jugal processes arched, nodose, long, and looped in middle, near extremely long, scooped jugal plates; 6-8 whorls in dorsomedially directed spiralia.

Remarks. The internal structure of this species shows remarkable jugal plates, the largest seen in any atrypid serially sectioned to date. The jugal processes are long and curved, but terminate in long, scooped jugal plates that almost reach the bottom of the dorsal valve. Whether this is an anomalously developed, pathologic jugal process system is not clear, as no others were sectioned for comparison. The sectioned Dudley specimen of *E. lonsdalei* (Alexander, 1949) did not yield jugal processes nor spiralia for comparison. This species is similar to the Wenlock species *E. lonsdalei* from the Dudley area in England, but appears to retain its deltidial plates and apical foramen throughout life; ribs are about the same size in both species, but shallower and more *Atrypa*-like in *E. lonsdalei*, and more distinct and tubular in *E. ekenia*. This species is the only atrypid to occur at Lau-

Fig. 38. *Endrea ekenia* n. sp. Statistical evaluation of specimens from 'Lau Backar 1', Eke beds, mid-Ludlow; depth peak at 7 mm, width peak at 14 mm; camera lucida, posterior detail of beak area in two specimens.

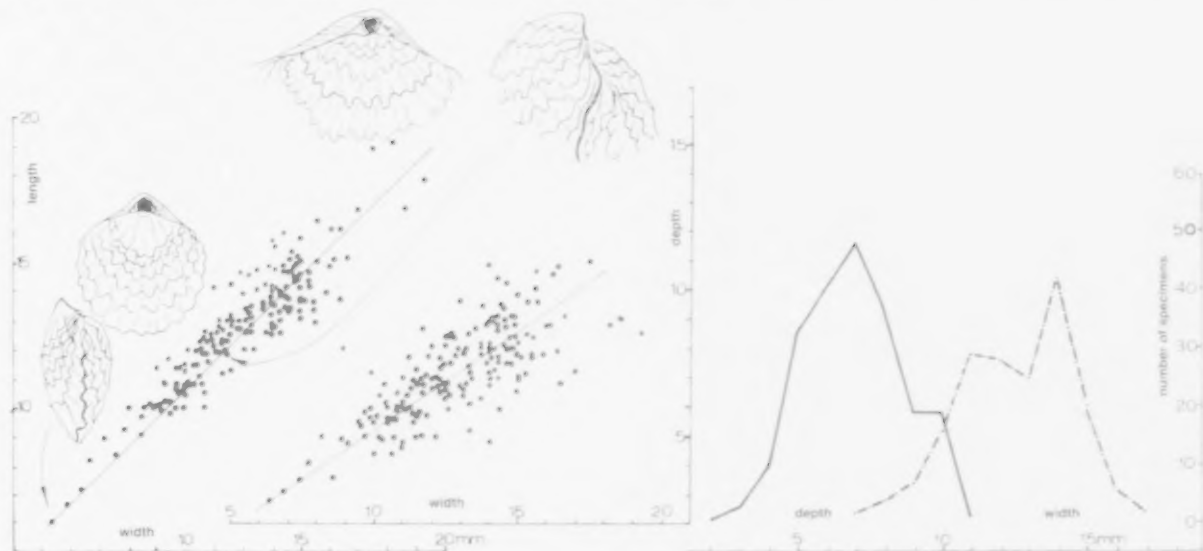
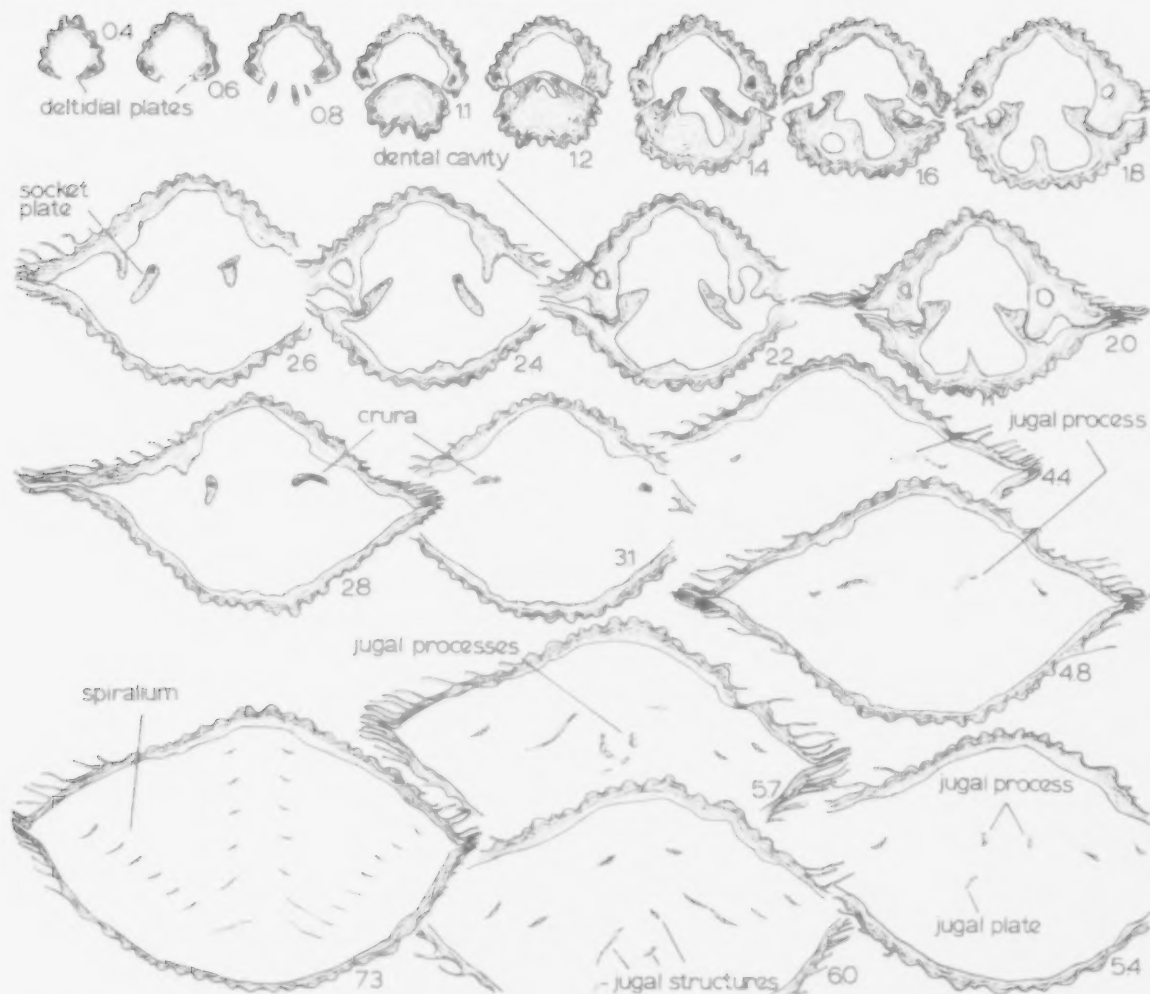


Fig. 39. *Endrea ekenia* n. sp. Serial sections of specimen from Lau Backar 1, Eke beds, mid-Ludlow; note the extensive projection of the jugal plates into the dorsal side of the shell cavity, prominent dental cavities, $\times 5$.



backar 1, the locus typicus. Several thousand well-preserved specimens of this atrypid species were collected when these outcrops were fresh. Both the Dudley and Laubackar species

Fig. 40. *Endrea ekenia* n. sp. Reconstruction of shell interior based on specimen serially sectioned (Fig. 39), Laubackar 1, Eke beds, mid-Ludlow, $\times 5$.



are distinct from *Endrea* of the Högklint and Slite beds in their shapes, micro-ornament, and more tubular ribs. The Gotland and British species show shape, rib, and growth lamella trends approaching the morphology of *Rugosatrypa* Rzhonsnitskaya 1975, from the Early Devonian of Eurasia. The occurrence of this globose, small species in the higher energy, shallower water biostromal-patch reefal facies of the Eke beds suggests it was adapted to life in coral thickets, possibly anchoring itself with its pedicle to corals or other substrate fragments. The species is absent in the *Rothpletzella* oncoid facies to the southwest, which favoured the large, convexoplane shell of the distinctly different species *Atrypa ulata* (Hisinger, 1831a).

Materials. Total more than a thousand shells from Laubackar (at the Riksmuseet there are drawers crowded full of this species; these were not measured); 180 specimens measured. **Eke Formation: Lau Backar 1** [= Lausbackar on map], Br104722-46 [25], Br150042-55 [14], Br43698-741 [43], [SW23: 36]; **Burgen 4**, Br104660-721 [62: atrypids appear to indicate this is the Eke beds, not Hemse beds].

Subfamily Atrypinellinae Copper, 2002b

Reticulatrypea Savage, 1970

Type species. *Reticulatrypea fairhillensis* Savage 1970, Early Devonian, Pragian, Australia.

Range. Ludlovian–Pragian, worldwide.

Diagnosis. Small to medium sized, generally elongate to rounded, biconvex, noncarinate; fine tubular–imbricate ribs (ribs spaced at >10–15 per 5 mm arc); regular, rhythmic overlapping growth lamellae, no frills; rib crests retreating into arcuate recesses, rib troughs extended into projections or spines; micro-ornament of fine concentric filae; distinct orthocline area, deltidial plates; rectimarginate to gentle anterior fold; interior lacking pedicle callist, but with dental cavities, slender teeth, delicate crura, jugal processes delicate, curving centrally to terminate in jugal plates which almost meet medially; spiralia with up to ca. 12 whorls.

Remarks. *Reticulatrypea* is a very small Pragian atrypid from Australia, and from Ludlow–Pridoli strata of the Great Basin area in Nevada. Both occurrences are known only from silicified material. Some of the detailed ornamental characters described in the diagnosis here therefore may not pertain to the type material (Dr. Norman Savage kindly provided silicified hypotypes from Australia for comparison). The discovery of similar specimens in Gotland suggests that the genus may extend down into the late Ludlow. Gotland specimens tend to be small to medium sized, and to have more prominent concentric growth lamellae, but the ribs are similarly also very fine and other characters of the beak and overall shape are comparable. Gotland specimens show the nature of jugal processes and spiralia for the first time, if indeed the generic assignment is correct. Remarkable is the large number of spiralia lamellae for such a small shell. *Reticulatrypea* is distinguished externally from *Endrea* in its small size, lacking frills, very fine, imbricate ribs, and having rib troughs extended as spines (as also in Llandovery *Gotatrypea*). Internally, *Endrea* has a much thicker shell, with moderate pedicle callist, thicker cardinalia, and a very different jugal process. It differs externally from *Gotatrypea* in having imbricate ribs and an orthocline area with deltidial plates, and internally by thin, delicate teeth, large dental cavities, and fine hinge plate. *Reticulatrypea* is similar to the Pridolian genus *Istokina* Breivel and Breivel 1988, and possibly a senior synonym of that, although the shell of *Istokina* seems more robust. *Reticulatrypea* also resembles some species normally assigned to the Pridoli–Emsian genus *Atrypinella* Khodalevich 1951, from which it appears to differ in lacking carination and bisulcation. *Atrypinella* also has a nodose shell, where rib crests and concentric lamellae intersect. Such a feature probably led to the development of fenestrae in the Punetatrypeinae, but fenestrae are not evident in either *Reticulatrypea* or *Istokina*. In China such species are commonly assigned to *Sibirispira*. It may be debatable whether to regard *Reticulatrypea* as a member of the Atrypinellinae or whether it is a side branch of the Atrypinae, which led to the Devonian *Desquamatia* group, via *Rugosatrypea*.

Species tentatively assigned.

Sibirispira amuna Fu 1982, Qinling Mountains, China, Ludlow–Pridoli.

- Reticulatrypea chattertoni* Lenz and Johnson 1985, Wellington area, Australia, Garra Fm., Lochkovian–Pragian (possesses strong overprinted ribs in the apical area).
?Atrypinella fixa Havlíček 1990, Prague Basin, lower Kopanina Fm., early Ludlow.
?Terebratula granulifera Barrande 1879, Czech Republic, Suchomasty Limestone, Emsian.
?Atrypa (Atrypinella) barba var. *losvensis* Khodalevich 1951, E slopes Urals, Lochkovian.
?Atrypa (Atrypinella) tumidula Khodalevich 1951, E slopes Urals, Early Devonian, Pragian.
?Spirigerina micula Richter, 1866, Thüringen, Germany, 'Tentakulitenschiefer', Ludlow.
Reticulatrypea neutra Johnson, Boucot, and Murphy, 1973, Birch Creek, Nevada, Pridoli [shows carination, overprinted ribs].
Reticulatrypea norrisi Lenz 1978, Royal Creek, Yukon, Canada, Road River Fm., late Lochkovian.
Reticulatrypea ryanensis Boucot, Johnson, and Zhang 1988, California, Hidden Valley Dolomite, Wenlock.
Sibirispira sparsa Rong, Zhang, and Chen 1987, Qinling Mountains, China, Pridoli.
Sibirispira striata Rong, Zhang, and Chen 1987, Qinling Mountains, China, Pridoli.
Reticulatrypea variabilis Johnson, Boucot, and Murphy, 1976, Nevada, D fauna, late Ludlow [non *R. variabilis* sensu Perry, 1984, pl. 30, figs. 35–59].

Reticulatrypea hamrae n. sp.

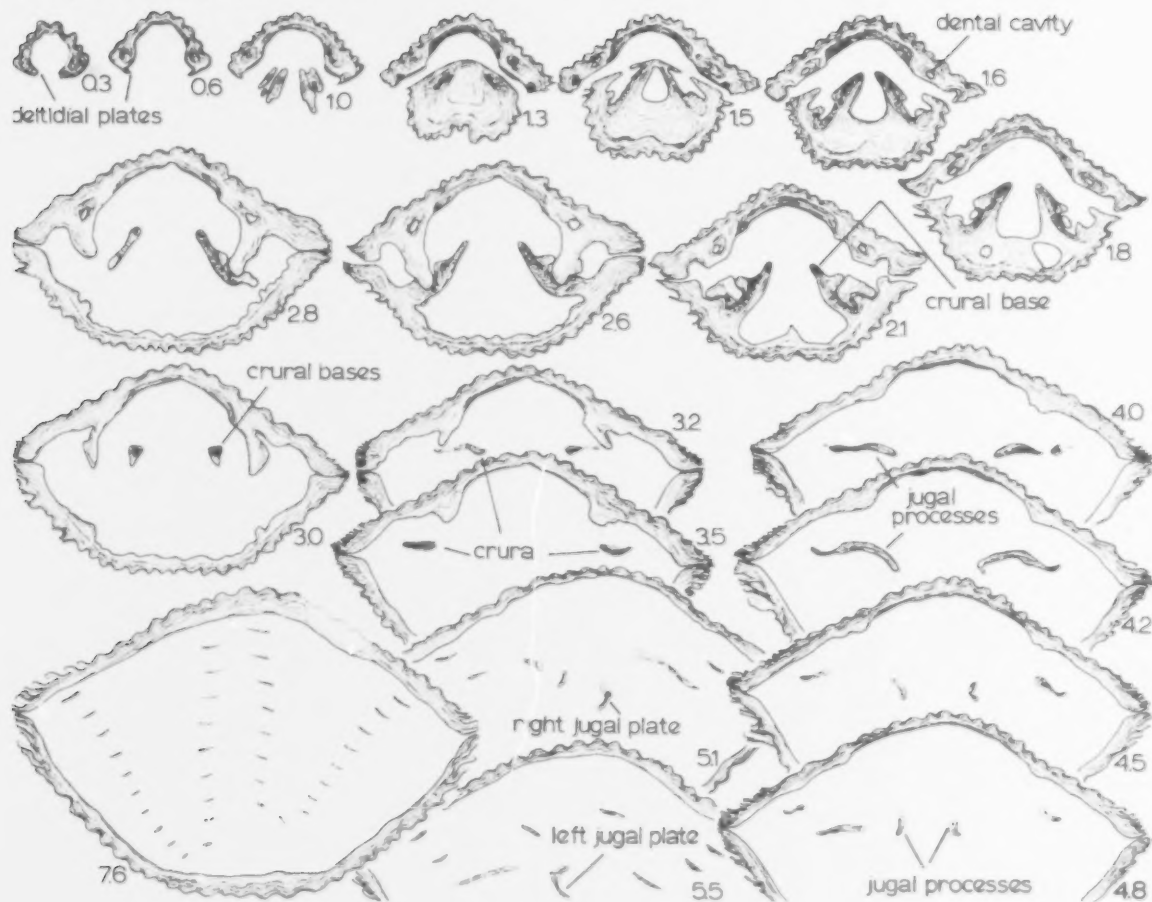
Pl. 17A, figs. a–n; Figs. 41–43

Type locality and stratum. 'Hoburg, V-sidan', shales of the Hamra Formation. The levels at which these specimens occur indicate the middle to high Whiteliffian, Ludfordian, latest Ludlow, probably within the *formosus* graptolite Zone. The material appears to be scarce in the reefal parts of the Hamra beds (which feature *Spirigerina quinquecostata*), but is more common in the inter-reef grainstone facies. The species is not abundant, and tends to be concentrated in nest-like occurrences.

Diagnosis. Elongate to rounded, equidimensional, 10–12 mm wide, moderately biconvex shells with slightly upturned growth lamellae; ribs fine, ca. 12 per 5 mm; small orthocline area, apical foramen, deltidial plates.

Description. Equidimensional, biconvex, slightly longer than wide to as wide as long, adult shells <20 mm wide (averaging 10–12 mm), depth <10 mm (averaging 5–8 mm); shield-shaped to rounded in outline, moderately indented hinge line; narrow apical angle in early growth stages, widening angle in adult stages; ribs fine, 11–13 ribs per 5 mm arc; growth lamellae short, spaced very regularly at 2.5–3 mm; ribs terminating in saw-edged margins with pseudo-spines doubling up at the margins of each recessed rib crest; ventral beak somewhat pointed; protruding, small orthocline area; small deltidial plates surrounding usually apical foramen (rarely transapical); anterior commissure usually rectimarginate, rarely very weakly plicate; shell interior with small,

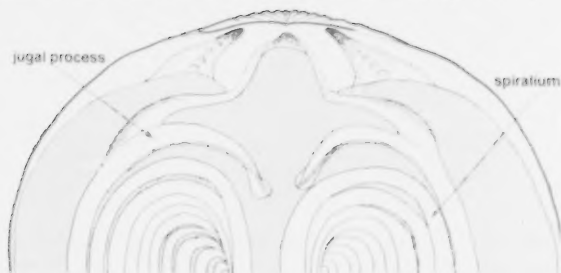
Fig. 41. *Reticulatrypea hamrae* n. sp., serial sections of typical mature shell, locality Hoburgen 2, late Ludlow. Note the distinct dental cavities, long teeth, and jugal processes. $\times 5$.



open, hollow deltoidal plates; teeth long, with rounded, central dental cavities, small lateral lobes; thin socket plates, with delicate inner socket ridges. Jugal processes and spiralia not sectioned.

Remarks. This is a rare shell, distinguished from the Australian type species *R. fairhillensis* Savage 1970 by being substantially larger (more than $2\times$ width), and by possessing clearly developed growth lamellae and projecting trough spines along the margins of adult shells. The spines seen on

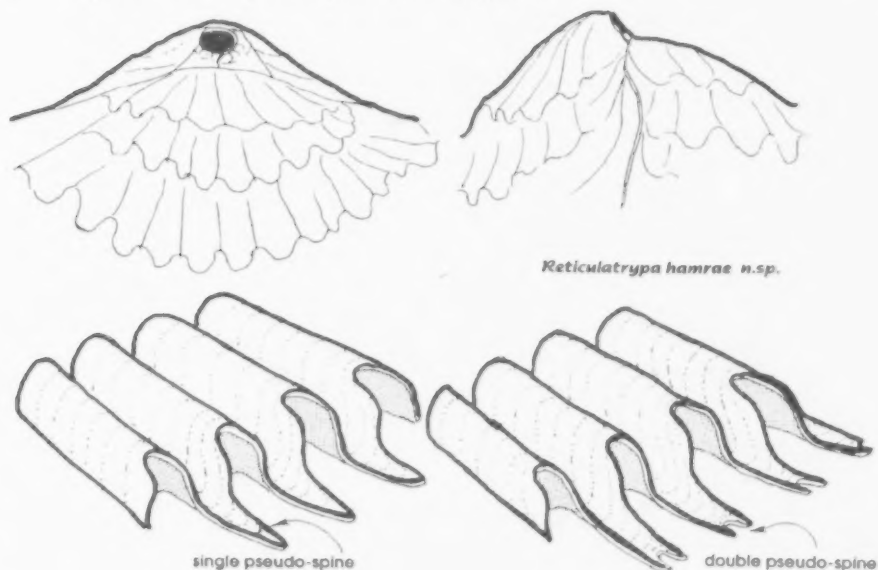
Fig. 42. *Reticulatrypea hamrae* n. sp., Hoburgen 2, late Ludlow; reconstruction of brachidia from serial sections (Fig. 41), $\times 6$.



the growth lamellae may be preserved as a single projection of the rib trough, or as a double projection, with the sides of the rib trough each forming one partial spine (Pl. 17A). This is partly a feature of preservation and partly a primary feature, as seen in Pl. 17A (figs. e, f) from the same specimen. Such structures are not evident on immature or very small specimens, and were perhaps not developed until the shell reached larger sizes. In Llandovery *Gotatrypea* such trough spines are also common, suggesting that the Atrypinellinae may have been derived directly from such Early Silurian stocks. Internal structures cannot be compared, as these are undescribed from all other species. Since the species is rather rare, inadequate material is available for statistical comparisons. *Spirigerina micula* Richter 1866, from the Tentakulturschiefer of northern Germany, is not available for comparison, as the types appear to be lost, and the figures and descriptions are inadequate.

Materials. 34 specimens. Type locality, 'Hoburgen, V-sidan, mergel', Br108064-76, 14 specimens; Br42694, 1; Hoburgen 2, west side, adjacent to small patch reef of the Hamra beds, with *Spirigerina quinquecostata* [SW35: 8]; Husryggen 1, top of shoreline bluffs, lower Hamra beds, ca. 2 m above Burgsvik Sandstone, [SW55: 6]; Kättelvik 1, Br108077-81 [5].

Fig. 43. *Reticulatrypa hamrae* n. sp. Hoburgren 2, late Ludlow; above, camera lucida drawing, highly magnified, of ventral umbo and foramen; below, growth of single and double 'pseudo-spines' in rib troughs, $\times 8$.



Family Atrypinidae McEwan, 1939
Subfamily Atrypinae McEwan, 1939
[= Gracianellinae Johnson, 1973]

Diagnosis. Minute to small atrypids, with marked ventral keel consisting of strong, ventral, divergent mid-rib pairs; small beaks, area with apical-transapical foramen; distinctive deltidial plates. Ribs usually distinct, relatively coarsely expanding (smooth, mature shells in some *Gracianella*); ribs continuous, or with rhythmic growth interruptions, or short growth lamellae; frills absent (but fibrose micro-ornament along commissure of *Guangyuania*); commissure generally weakly sulcate-rectimarginate, rarely weakly plicate. Teeth short, simple with dental nuclei; thick hinge plate, inner socket ridges commonly conjunct to almost fused centrally; disconnected to nearly fused jugal processes ending in small, rounded jugal plates; spiralia of fewer than 6–7 whorls, directed dorsomedially to mediodorsally.

Genera assigned. *Atrypina* (*Atrypina*) Hall and Clarke 1893; *Atrypina* (*Atrypinopsis*) Rong and Yang 1981; *Gracianella* (*Gracianella*) Johnson and Boucot 1967; *Gracianella* (*Sublepidia*) Mizens and Sapelnikov 1982; *Gracianella* (*Guangyuania*) Sheng 1975. [Consult Copper, 2002b, for Treatise usage.]

Range. ?Late Ashgill (Hirnantian) – Llandovery – Emsian. *Atrypina* from the Ashgill are not yet verified, and may be small species or specimens of *Eospirigerina* (*Spirigerininae*), or possibly a new genus, as seen from Hirnantian specimens of *Anticosti* [cf. '*Atrypina gamachiana*' Twenhöfel, 1928]. Reed (1897) reported the species *Atrypina similis* from the Hirnantian Keisley Limestone of Britain, but this has not been re-examined or sectioned to date.

Remarks. This subfamily includes species ranging from weakly imbricate to tubular, uninterrupted ribs, and commonly

strong ventral carination. Some species of *Gracianella* (*Gracianella*) show rib loss. Late Llandovery *Gracianella* (*Guangyuania*) from China have ventral carination and ribs only on the apical shell portions. Thus some members of this group have even lost their ribbing, or possibly started off with a nearly smooth shell to develop ribbing later. Species of atrypids now assigned to *Gracianella* (*Sublepidia*) were described as *Atrypina* by Hall (1893, p. 162), who was early to note similarities. *Gracianella* has sometimes been assigned to the Carinatininae (Johnson and Boucot, 1972), or to its own subfamily, the Gracianellinae, by Johnson (1973). Its carination, regular growth lamellae, and unusual hinge plate suggest such an early transition. *Gracianella* are distinct from *Atrypina* primarily by a somewhat larger and more protruding beak, orthocline area, and most are similar in having strong ventral mid-rib carination at the shell apex. The ancestry of the subfamily lies clearly with the *Spirigerininae*, via neotenus retention of the early growth stage. In turn, the Atrypinae may have given rise to several important atrypid stocks, the Karpinskiinae via *Crassatrypa* in the Ludlow–Pridoli, and to the Carinatininae by Pridoli time (as intimated by Johnson, 1967).

Atrypina (*Atrypina*) Hall, in Hall and Clarke, 1893

Type species. *Leptocoelia imbricata* Hall 1859, 'Shaly Limestone, Lower Helderberg group', Clarksville, New York, Early Devonian, ?Pragian–Emsian [see also Hall, 1859, 1861].

Diagnosis. Minute to small, ventribiconvex–planoconvex, rarely subconcavoconvex; strong ventral carination due to

mid-rib pair producing small anterior sulcus (commissure commonly sulcate to rectimarginate); smooth ribs or short, rhythmic growth lamellae; small area, minute apical foramen (rarely transapical), with or without deltidial plates; strongly incurved beak in adult shells; small anacline area. Internally, thick-shelled wall, minute dental cavities or notches; short deltidial plates; stout teeth; thick hinge plates commonly fused to form an irregular, thickened pad; cardinal pit recessed; strong dorsal median septum; crural bases minute; relatively few (<6) spirallial whorls, dorsomedially directed; jugal processes touching or nearly fused.

Remarks. *Atrypina* appears to be generally rare in Gotland and the eastern Baltic, but it is a common constituent of the Wenlock sequence in Britain. There is a trend in reduction of ribs (or increase in rib size), and decrease in shell size from the basal to upper Wenlock succession, and into the Ludlow, as seen in the change from *A. buildwasensis* to *A. barrandii*. The smallest shells came from the Hamra beds. This contrasts with an increase in relative rib size in *Spirigerina*, *Xanthea*, and *Eospinatrypa* during the Wenlock. The Llandovery (Aeronian) subgenus *Atrypinopsis* Rong and Yang (1981) appears to occur only in China: the sole difference is a dorsal fold (probably simply by enlargement and elevation of the space between the ventral mid-rib pair), and more biconvex shell. A similar commissure sulcation, with central ridge, is evident, for example, in *Atrypina buildwasensis*. *Atrypinopsis* is suggested to be a subgenus level taxon. It should be noted that the Early Devonian type species of *Atrypina*, *A. imbricata* (Hall, 1859), usually has a biconvex shell, unlike the planoconvex shell of most Silurian species, and is much less earinate. Thus the only real difference between *Atrypina* and *Atrypinopsis* lies in the development of a dorsal fold in *Atrypinopsis*. It seems inadvisable at present to create yet a third subgenus to accommodate the bulk of the Silurian planoconvex species, as differences are apparently gradational. *Atrypina* (*Atrypina*) is not confirmed from Llandovery rocks, except in China (Rong and Yang 1981), where it is said to co-occur with *Atrypinopsis*. The species '*Atrypina*' *gamachiana* was reported by Twenhofel (1928) from late Ashgill (Hirnantian) Ellis Bay Formation of Anticosti Island, Canada. This species is unlike *Atrypina* in its smooth undulations, instead of ribs, and may be affiliated with the species *Becscia scissura* (Copper, 1995). '*Atrypina*' *similis* Reed 1897, from the Hirnantian Keisley Limestone of Britain, may belong to *Zygospira* (according to Cocks, 1978). *Gracianella* does not occur in the Baltic Basin, Podolia, or Britain, although it is a common constituent of Wenlock–Pridoli sections in the Urals, the Czech Republic, Carnic Alps, and western and arctic North America. There are as yet no details available on the internal structure of *Gracianella*, as the Nevada types are silicified. British species such as *Atrypina buildwasensis* could be mistaken for *Gracianella* (*Sublepidia*). This monograph includes the first serial sections made of any *Atrypina* species.

Range and distribution. Late Ashgill (Hirnantian) – Emsian, worldwide, except Gondwana.

Species tentatively assigned [total 26 species].

Retzia barrandii Davidson 1848, Hayhead, Walsall, Dudley Limestone, late Wenlock.

Atrypina chattertoni Perry, 1984, Yukon, Canada, 62–68 m below top of Delorme Fm., Emsian.

Atrypina clintoni Hall and Clarke 1893, 'drift of western New York', Clinton Fm., late Llandovery.

Ogilviella ?damoensis Su, Rong, and Li 1983, Bateobao, inner Mongolia, Ludlow.

?Carinata diana Kulkov 1974, NW Altai, Chinetin Horizon, late Llandovery (?small *Spirigerina*).

?Atrypina dichotoma Kulkov 1974, Kamysenskogo, Altai, Chinetin Horizon, Yarov beds, late Llandovery.

Atrypa disparilis Hall 1852, Wolcott, Wayne County, Indiana, 'Niagara Shale', Wenlock.

Atrypina eremita Havlíček 1999, Prague Basin, Lochkov Fm., Lochkovian.

Atrypina erugata Amsden 1968, Batesville, Arkansas, St. Clair Limestone, Wenlock.

Atrypina (?) *frequens* Menakova 1964, Daurich, Zeravshan–Gissar Mtns., Bed K, Wenlock.

Rhynchonella gallina Haupt 1878, erratic boulders, 'weichen Kalke', north Germany, Ludlow.

Atrypina gramma Rong, Xu, and Yang 1974, S China, middle Llandovery.

Atrypina hami Amsden 1958a, White Mound, Oklahoma, Haragan Fm., '29–36 ft.' above base, Lochkovian.

Leptocoelia imbricata Hall 1859, Lower Helderberg, Clarksville, New York, ?Pragian–Emsian.

Atrypina inops Havlíček 1999, Prague Basin, upper Kopanina Fm., Kosov Hill, late Ludlow.

?Protozeuga insueta Oradovskaya 1983, Neznakomki River, Omulev, NE USSR, Chalmak Horizon, early Llandovery (possibly = *Becscia*).

?Atrypina jakubinka Havlíček 1991, Prague Basin, Zelkovic Fm., Hyskov, middle Llandovery.

?Zygospira jupiterensis Twenhofel 1928, Jupiter River, Anticosti, Gun River Fm., Aeronian (possibly *Spirigerina*).

?Atrypa lamellata Hall 1852, Schoharie, New York, 'Coral-line Limestone', Early Devonian.

Atrypina latesinuata Rong, Xu, and Yang 1974, South China, middle Llandovery.

Atrypina magnaventra Grubbs 1939, Chicago area, Illinois, Niagaran Dolomite, Wenlock.

Atrypina paulula Havlíček 1990, Prague Basin, Motol Fm., late Wenlock.

Atrypina prosimpsoni Johnson, Boucot, and Murphy 1973, Willow Creek, Nevada, 'F fauna', Lochkovian.

Atrypina similis Reed 1897, Kildare, Britain, Keisley Limestone, Hirnantian.

Atrypina simpsoni Johnson 1970, Coal Canyon, Nevada, *Quadrithyrus* Zone, early Pragian.

Atrypina talenti Savage 1970, New South Wales, Mandagery Park Fm., late Lochkovian.

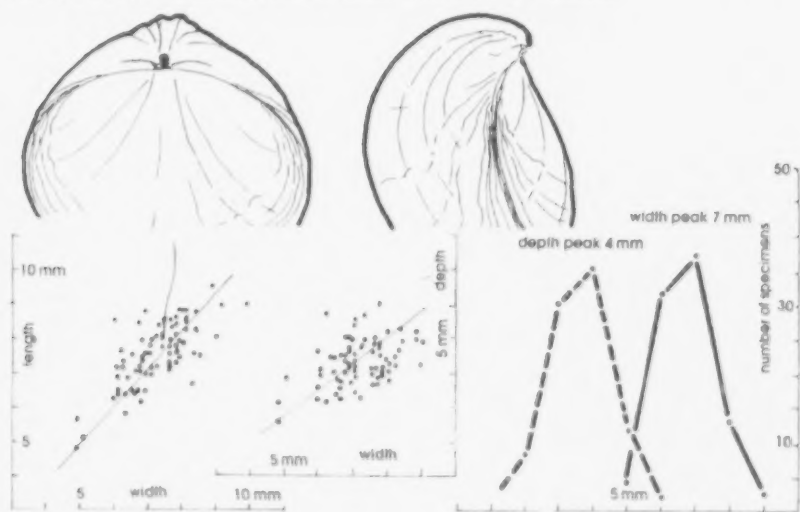
Atrypina (*Atrypina*) *buildwasensis* n. sp.

Pl. 17B, figs. a–t; Fig. 44

1867 *Retzia ?barrandii* Davidson, sensu Davidson, pl. 13, figs. 10–11.

Type locality and stratum. 'Buildwas', at Wenlock Edge (Davidson, 1867), and Buildwas Shale (30 m thick), approximately *murchisoni* to lowest *riccartonensis* zones, early–

Fig. 44. *Atrypina* (*Atrypina*) *buildwasensis* n. sp. Statistical evaluation pooled from all specimens labeled as derived from the Buildwas beds, 'Buildwas', early Wenlock; compare with *Atrypina barrandii* from the late Wenlock.



middle Sheinwoodian, early Wenlock. No more precise locality data is available.

Diagnosis. *Atrypina* of moderate size (average width 7 mm, average depth 4 mm), somewhat elongate, globose; strongly convex vv with keel formed by enlarged mid-rib pair, weakly biconvex dv; 6–10 ribs on dv; generally distinct, very short growth interruptions to growth lamellae; anacline to hypercline area, transapical foramen, obscured deltidial plates; commissure weakly sulcate, with medial rib forming ridge in centre of sulcus.

Description. Shell outline ovate to somewhat elongate, globose, with straight shoulder line, apical angles 110° – 125° ; shells up to 8.5 mm wide, longer than wide, up to 5 mm deep; vv strongly convex, keeled due to strong ventral mid-ribs, dv slightly convex, less commonly planar. Small area hypercline, pressed against dorsal valve; deltidial plates inwardly retracted, transapical, small, round foramen. Small, dorsal V-shaped fold produced by depression between ventral mid-rib pair and crested by single dorsal mid-rib; ribs straight, distally expanding; vv dominated by inflated central mid-rib pair flanked by 3–4 small lateral ribs rarely bifurcating; dv with equally sized ribs, single mid-rib with usually 3 to rarely 4 lateral ribs; first growth lamellae distinct at 4–5 mm from umbo, then rhythmic at 0.5–0.8 mm spacing to crowding at commissure; growth lamellae hug shell surface on both valves and are barely upturned. No micro-growth lines observed.

Teeth stout, with minute apical dental cavities, expanding anteriorly, weak lateral dental lobe; deltidial plates solid, normally pushed interiorly, lining pedicle cavity. Dorsal valve with minute notothyrial pit, commonly sealed by inward, continuous overgrowth of inner socket ridges; expanded growth of inner socket ridge abutting teeth; cardinal process absent; hinge plate thick; crural bases bulbous; delicate crura laterally directed; strong carinate median septum. Spiralia, jugal processes not observed in sections prepared.

Remarks. *Atrypina buildwasensis* is easily distinguished from its younger, late Wenlock relative *A. barrandii* by its larger shell (nearly 50% wider), greater number of ribs, strong, keeled ventral mid-rib pair, presence of abundant growth interruptions or short growth lamellae, and its hypercline beak. There are some similarities to *A. disparilis* (Hall, 1852), in having 3–4 ribs flanking the dorsal mid-rib, but *disparilis* is not so inflated ventrally and has an orthocline beak and apical foramen. The Hall types, which were examined, also show a larger population proportion of shells with fewer ribs, and the Hall species falls somewhere between *buildwasensis* and *barrandii* in morphology. *A. talenti* (Savage, 1970) differs in lacking growth lamellae and in its outline and beak structure. Of the late Llandovery Chinese species, *A. (Atrypinopsis) gramma* Rong, Xu, and Yang 1974 has a bifurcating dorsal mid-rib and *A. latesiniata* Rong, Xu, and Yang 1974 is a wider, less convex shell with a strong dorsal mid-rib. The Chinese species have, however, about the rib count of *A. buildwasensis*, which also has a weak dorsal fold than seen in *Atrypinopsis*.

A. buildwasensis is absent on Gotland. The mode of life of this *Atrypina* species was probably liberosessile, with the ventral valve on the underside, and the shell slightly buried with its keel in the substrate. This is evidenced by the hypercline beak, loss of or reduction of foramen, and the encrusting epibionts, which tend to be mostly on the dorsal valve. *Atrypina buildwasensis* comes from a deeper water, muddy facies, implying a soft substrate. No equivalent forms were discovered in Gotland collections, e.g., from the Höglint or Slite beds, where *Atrypina* is absent, possibly implying that water depths were too shallow there.

Materials. Total 220 specimens from the 'Lower Wenlock Shale', i.e., the Buildwas beds. **Buildwas**, BB20799 [8], BB34745 [31], B34746 [20], B34747 [41], B4961 [2], B24139 [3], B1593 [50], B1098 [16], B3209 [3], BB60884–5 [2], BB553435–6 [2], BB55143 [1], BB20799 [8], A26539–54 [16], A28901–3 [3], GSM103764–81 [20].

Atrypina (Atrypina) barrandii (Davidson, 1848)

Pl. 18A, figs. a-m; Figs. 45-48

1848 *Terebratulula barrandii* Davidson, p. 332, pl. 3, figs. 32 (5 views).1867 *Retzia ?barrandii*, Davidson, p. 128-129 (partim), pl. 13, figs. 13, 13a-d.1879 *Retzia barrandei* [sic], Barrande, pl. 82, figs. 4:1-6.?1881b *Atrypa barrandii* [sic], Davidson, figs. 11-12.?1882 *Atrypa barrandei* [sic], Davidson, p. 114-115, pl. 7, figs. 7, 7a-b [N.B. the species name has been spelled three different ways, and the first name is used here].

Type locality and stratum. 'Les couches du Wenlock Limestone de Hay head, près Walsall' and 'Wenlock Limestone or Shale at Hay Head, near Walsall' (Davidson, 1848, latter is the original label on lectotypes in Davidson collection). The exact collecting level in the West Midlands appears unknown, and no new collections are available from 'Hay Head'. Bassett (1974) correlated the upper Dudley (Wenlock) Limestone here with the *ludensis* Zone, but the type horizon is probably the *nassa* Zone, and may be as low as the upper *lundgreni* Zone. The species is also common at Wenlock Edge in the 'Tickwood beds' [= Farley Mbr., Coalbrookdale Fm.], just below the Much Wenlock Limestone, from the *nassa* Zone [mid-Homerian, late Wenlock]. Davidson (1867) also cited occurrences at Buildwas, but this refers to *A. buildwasensis* n. sp. from the lower Wenlock. On Gotland this species is identified from the island locality 'Utholmen' and around Västergarn (Idå 1), in strata labeled as upper Slite beds, but it is not known from the Mulde Marl. It is also present in the Klinteberg beds at Hunninge 1.

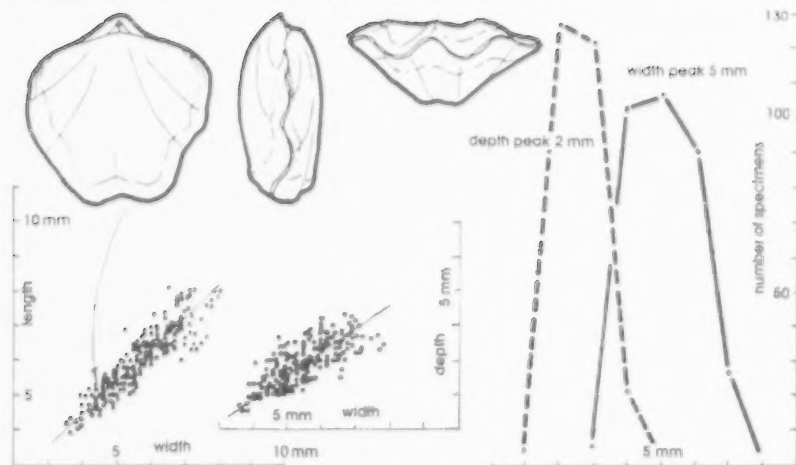
Diagnosis. Small biconvex to ventribiconvex *Atrypina* (average width <5 mm; peak depth <3 mm), longer than wide, with small, orthocline to weakly anacline area, apical to slightly transapical foramen, deltidial plates exposed; normally 5 ribs dv, 6 ribs vv; growth lamellae, interruptions absent; commissure rectimarginate.

Description. Shell slightly ventribiconvex to biconvex, less commonly planoconvex, elongate to more rounded; slightly longer than wide (max. length 8 mm, widths 4-6 mm, rarely 7 mm, averaging <5 mm; depths 2-4 mm, av. <3 mm); rounded hinge corners; straight to weakly indented shoulder line. Beak small, protruding; area orthocline to weakly anacline, rarely apsacline; small foramen normally apical, rarely penetrating umbo. Ribs coarse, expanding distally, with 5, to less commonly 7 ribs, on dv, single central mid-rib strong, undivided; ventral mid-rib pair expanded, V-shaped, forming sulcus and producing weak carination; growth lamellae or interruptions absent. Commissure rectimarginate.

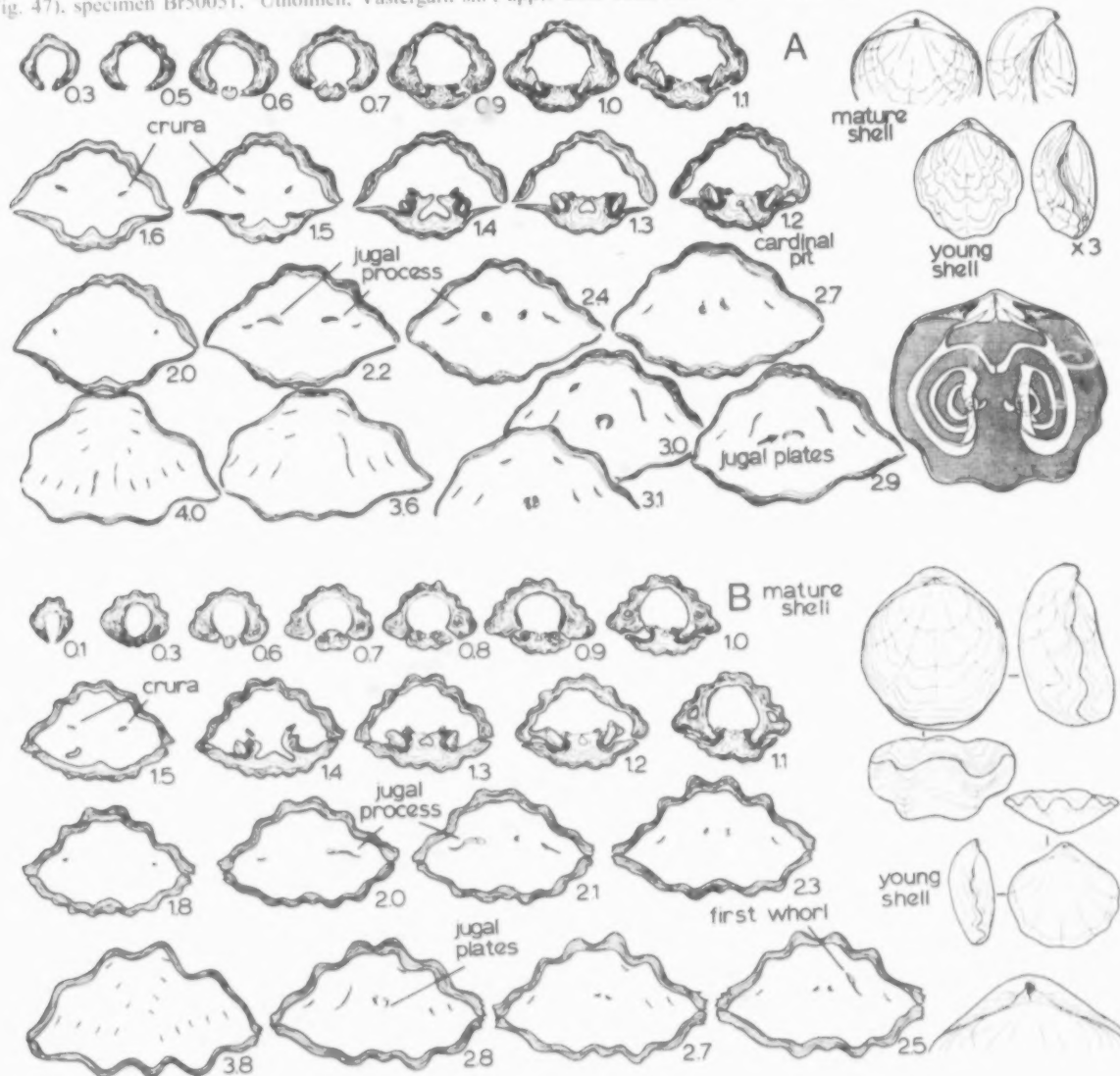
Ventral valve with small but thick, solid deltidial plates fastened to side of pedicle cavity; small, slit-like to rounded dental cavities; teeth subhorizontally directed towards shell centre with dental cavities opened to ventral side; poorly developed to absent dental lateral lobes. Hinge plate thick, commonly fused and arched over rounded cardinal pit; socket relatively deep. Crural bases round, thick, giving rise to laterally directed stubby crura; jugal processes arched, thick, tipped by small, curved jugal plates almost meeting in the centre; spiralia with 3-4 revolutions directed dorso-medially (for spiralia see also Davidson, 1881b).

Remarks. *A. barrandii* is identifiable by its smaller size (ca. 50% smaller), wider and thinner shell, tendency towards planoconvex shell, and has an orthocline area, with exposed apical foramen and deltidial plates. Davidson (1867) included both species herein described under the single name *A. barrandii*, and thus his description is broader than this revised version. The specimens prepared by Glass (Davidson, 1881a, b), to demonstrate spiralia, came from the 'Tickwood beds' (i.e., upper Coalbrookdale Fm.). The distribution of this species in the [probably uppermost] Wenlock Shale at Walsall, and the [probably lowermost] 'Much Wenlock Limestone, Dudley', suggests that these strata are assignable to the *nassa* Zone, but *Atrypina barrandii* may have a longer range. On Gotland, this species is also recognizable in the lower Klinteberg beds. *Atrypina* collected from glacial errat-

Fig. 45. *Atrypina (Atrypina) barrandii* (Davidson, 1848). Statistical evaluation of specimens combined from the 'Wenlock Shale, Walsall' and 'Wenlock Limestone, Dudley', probably from the same stratigraphic levels, despite the labels, i.e., the Farley Mbr., Coalbrookdale equivalents at Wenlock Edge, as seen from specimens at Tickwood, late Wenlock.



Figs. 46, 47. *Atrypina (Atrypina) barrandii* (Davidson, 1848). Serial sections of A (= Fig. 46), BB34794 ['Farley Dingle, Tickwood beds', late Wenlock], demonstrating typical internal features ($\times 5$), and camera lucida drawings of neanic, and mature shells; B (= Fig. 47), specimen Br50051, 'Utholmen, Västergarn sn.', upper Slite beds, mid-late Wenlock, $\times 5$.

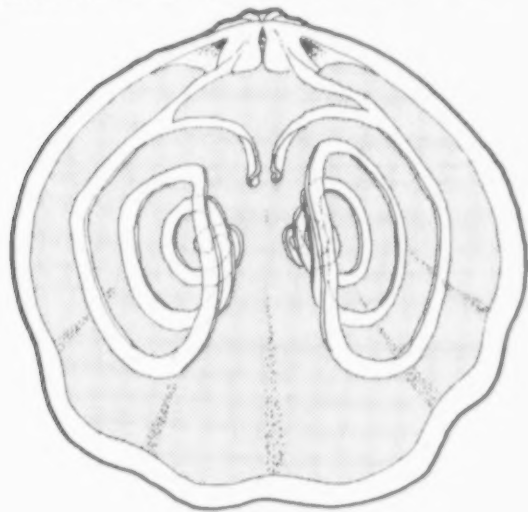


ics of north Germany (possibly derived from Gotland strata), '*Rhynchonella*' *gallina* Haupt 1878, cannot be compared adequately, as the types are lost, and the original description is incomplete [see below]. However, Gotland material suggests that *A. cf. gallina* is even smaller in size.

Materials. About 550 specimens from the upper Wenlock (Farley Mbr., Coalbrookdale Fm. to Much Wenlock Limestone). 'Wenlock Shale, Hay Head, Walsall', probably from Tickwood beds equivalent, A26507-38 [32], B942-5 [4], B70204-7 [4]; 'Wenlock Limestone, Dudley', A26555-75 [21], B23224 [5], B589 [29], B24025 [1]; 'Wenlock Shale, Dudley', B27091 [14]; 'Tickwood beds near Tickwood', BB61053-6 [4], BB103847-922 [75]; 'Tickwood beds, Dale Coppice, Coalbrookdale',

BB70151-2 [2]; 'Tickwood beds, roadside above railway bridge between Tickwood and Farley Dingle, loc. 42' (consult Davidson, 1881b), BB61022-21 [20], BB34793-4 [2], B34743 [1], B34744 [ca. 100], B34923 [4]; 'Wenlock Shale, W Tickwood' BB70157-8 [2], BB70161 [1], BB1583 [231]. On Gotland, this species occurs in the middle to upper *Slite beds*: *Utholmen* [this locality was known to Lindström, Angelin, and Munthe, and material was collected along the shoreline at low tide in upper Slite strata, according to Jaanusson, 1986], Västergarn sn. Br50001-2 [2], Br50034-52 [19]; *Idå 1*, Västergarn sn. [12 specimens, uncatalogued]; *Klinteberg beds* (low-middle); *Hunninge 1*, Klinte sn., Br134682-91 [6]; *Lilla Karlsö*, Br134578-134618 [41]; these specimens are all minute, <3 mm wide, and questionably assigned].

Fig. 48. *Atrypina* (*Atrypina*) *barrandii* (Davidson, 1848). Reconstruction from serial sections of hypotype BB34794, 'Farley Dingle, Tickwood beds', late Wenlock. From Fig. 47, $\times 5$ [see Fig. 46].



Atrypina cf. *gallina* (Haupt, 1878)
Pl. 18B, figs. a-m

1878 *Rhynchonella gallina* Haupt, p. 73, pl. 2, figs. 16a-e [see Pl. 18B, figs. h, i].

Type locality and stratum. North German glacial erratic boulder terrain, 'Silurische Sedimentärgeschiebe, weichen Kalke' [glacial erratics, soft limestone]: Haupt, 1878. The precise collecting locality was not defined by the author, but this is probably not relevant, as the boulders were very likely derived from southern Gotland, or seabed outcrops south of Gotland. Specimens virtually identical to the illustrated fig-

ures of Haupt (1878) occur in the Hamra-Sundre sequence (late Ludfordian, *formosus* Zone, late Ludlow). From the 'Atrypina beds' at Builth, which are 30-45 m thick and lie in the *tumescens-incipiens* Zone of Gorstian age (early Ludlow), there are other small specimens reported (Calef and Hancock, 1974; Lawson, 1975) that may belong to this species. Their identity cannot be confirmed, as collections were not available.

Description. Minute to small shells, almost equally wide as long, maximum width 4.8 mm, (average 3.8 mm); maximum length 4.8 mm (average 3.6 mm); average depth 1.9 mm [data based on Kattelviken 1]; protruding beak; small orthocline area with flanking deltidial plates, apical-transapical foramen; 4-6 ribs ventral valve (normally 4 ventral ribs), with mid-rib pair slightly expanded; 5 ribs on dorsal valve, with weaker rib lining sulcus; commissure sulcate. Interior of both valves with commissural rim; interior dv with narrow cardinal pit; vv with short, stubby teeth. Serial sections not prepared.

Remarks. Haupt (1878) described and figured specimens from glacial erratics of northern Germany that were 'less than 4 mm wide and 5 mm long', with two strong ventral mid-ribs flanked by two smaller lateral ribs. This description fits specimens from the Hamra beds of Gotland, but a single specimen from the Eke beds, although also small in size, had 7 ribs on the vv, and is thus only tentatively assigned here. Although some specimens from the Klinteberg beds are also very small, and also have relatively few ribs, these are probably immature specimens, and have been assigned to *Atrypina barrandii* (Davidson, 1848). If a larger collection of *Atrypina* becomes available from the Hamra beds, or equivalent strata in Britain, it may be worth redescription.

Materials. Total 46 specimens. *Hamra beds*: **Kattelviken 1**, Vamlingbo sn., Br134661-74 [15 specimens]; **Grumpvik**, Vamlingbo sn., Br125153-67 [15]; **Burgsvik**, Öja sn., Br50025-30 [6], Br125146-51 [6]; **Hoburg, V-sidan**, Sundre sn., Br48001-003 [3]; *Eke beds*: **S om Bomunds i Burgen**, När sn., Br125168 [1].

Subfamily Plectatrypinae Copper, 1996b

Plectatrypa Schuchert and Cooper, 1930
[= *Imbricatospira* Fu, 1982]

Diagnosis. Small to medium-sized, biconvex-dorsibiconvex, globose shells, short-hinged; normally carinate to subcarinate ventrally due to expanded, divergent mid-ribs; well-developed dorsal fold; macro-ornamentation of closely spaced imbricate growth lamellae, sometimes protruding as capidulae or aborted spinose growth; beak small, protruding; short, usually anacline area; foramen apical-transapical; lacking a pedicle callist; well-developed deltidial plates; teeth with minute dental nuclei, lacking dental cavities; simple, curved jugal processes; spiralia of fewer than 10 whorls.

Genera included. *Plectatrypa* (*Plectatrypa*) Schuchert and Cooper 1930 [= *Imbricatospira* Fu 1982]; *Plectatrypa* (*Gutnia*) Copper 1995; *Sypharotrypa* Copper 1982; *Xanthea* Copper 1996b. Excluded taxa are: *Paraplectatrypa* Zeng et al. 1993, nomen nudum, = *Spirigerina*; *Megaplectatrypa* Zhang 1981, Early Devonian, Dzungar, NW China (a probable karpinskiinid).

Range. Early Llandovery (Rhuddanian) - Pridoli.

Type species. *Terebratula imbricata* J. de C. Sowerby 1839, Much Wenlock Lst., late Wenlock.

Range and distribution. Worldwide, Llandovery (?Rhuddanian-Aeronian) - Ludlow. The genus has been reported from Late Ordovician strata (e.g., Reed, 1944; Temple, 1970), but these specimens do not include the truly imbricate shells of *Plectatrypa* and are probably assignable to *Eospirigerina* (see Cocks, 1978), or *Schachriomonia*. The upper limit of the genus range is uncertain: it reached a peak in the Wenlock and is probably not present beyond the Ludlow. In Britain the genus is rare until Wenlock time. On Anticosti Island, it occurs only in the highest formation, the Chicotte, of Telychian age, and is absent in the earlier Llandovery.

Diagnosis. Globose, dorsibiconvex, relatively small to medium size; normally incurved, anacline area, obscuring del-

tidial plates (retracted into the pedicle cavity); relatively prominent ventral double carination; sharp U-shaped dorsal fold; distinctive, closely spaced, imbricate, fine to coarse ribs; short growth lamellae. Internally, lack of pedicle callist, retraction of deltidial plates into pedicle cavity; solid teeth, or teeth with minute dental nuclei offset to the inner shell wall; central to ventral jugal processes ending in minute jugal plates; dorsally directed spiralia fewer than 8 whorls.

Remarks. *Plectatrypa* is distinguished from *Xanthea* (Copper, 1996b) and *Sypharotrypa* (Copper, 1982) by its distinctive closely spaced shell imbrication, fine to medium ribs, and shell outline. The latter genus seems the probable ancestor, considering its presence in the early Llandovery. *Plectatrypa* is readily distinguished from contemporary *Spirigerina* by its imbricate growth lamellae. The late Llandovery genus *Imbricatospira* Fu 1982 has the strong ventral mid-rib carination and imbricate ribs of *Plectatrypa*, and thereby appears synonymous. Fu (1982, 1985) stated that it is like *Clintonella* except for imbrication: this could not be confirmed. The genus *Clintonella* was extinct by the latest Llandovery.

Plectatrypa (*Plectatrypa*) Schuchert and Cooper, 1930

Diagnosis. As for genus, but ribs medium sized, strong carination, sharp anterior U-shaped fold, imbricate, intersected by short, upturned, even growth lamellae; capidulae unknown.

Range and distribution. Llandovery-Ludlow, ?Pridoli.

Remarks. *Spirigerina* from Europe were commonly assigned to the Schuchert and Cooper genus *Plectatrypa* until Alekseeva (1960b) correctly pointed out the important differences between these two genera, now assigned to different subfamilies. *Plectatrypa* is divided into two subgenera: *Plectatrypa* (*Plectatrypa*) and *Plectatrypa* (*Gutnia*). *Plectatrypa* (*Plectatrypa*) is distinguished from *Plectatrypa* (*Gutnia*) by its coarser ribs and lack of pseudo-spinose, capidulate ornament, but when this ornament is not preserved *Gutnia* resembles a finely ribbed form of *Plectatrypa* (when the shells co-occur, they are readily separable). *Gutnia* also has a less well-defined fold and sulcus and poorly defined mid-rib pair on the ventral valve. True *Plectatrypa* in Gotland and Britain appear to be common only in rocks of late Llandovery to Wenlock age, and fewer *Plectatrypa* are noted from the Ludlow and Pridoli, suggesting a Late Silurian decline.

From Gotland to England, *Plectatrypa* (*Plectatrypa*) evolved initially as a smaller shell with a somewhat straight hinge and finer ribs in early Wenlock time (*P. abbreviata*) to a rounded, more globose, and larger shell (*P. parimbricata*). It is not found in highest Wenlock strata on Gotland, but the late Wenlock type species *P. imbricata*, from Britain, is smaller than its presumably ancestral form from the older Slite beds and Upper Visby beds, and has ribs covering the entire fold and sulcus. The size trend is the opposite of that seen in *Atrypina*. *Plectatrypa* generally occurs in deeper, shaly, distal shelf facies on western Gotland, but *Gutnia* is associated with small coral patch reefs in the northeast, proximal shelf, Slite facies.

Species tentatively included.

Imbricatospira decora Fu 1982, Tongxin, Ningxia province, late Llandovery [see also Fu, 1985].

?*Atrypa expansa* Lindström 1880, SW Sweden, ?middle Llandovery.

?*Atrypa flexuosa* Marr and Nicholson 1888, Skelgill, Scotland, lower Skelgill beds, Rhuddanian [?possibly = *Sypharotrypa*].

Plectatrypa henningsmoeni Boucot and Johnson 1967, Oslo area, Norway, Rhuddanian, Llandovery.

Plectatrypa parimbricata n. sp. Gotland, Slite beds, Wenlock.

Spirigerina (*Eospirigerina*) *porkuniana* Jaanusson, in Rubel 1970, Estonia, Juuru Horizon, Rhuddanian, Llandovery.

Atrypa rugosa Hall 1852, Lockport, New York, 'shale of the Niagara Group', Wenlock.

Plectatrypa wenlockiana Lopushinskaya 1976 [see also 1965], northern Siberian Platform, Wenlock.

Excluded species.

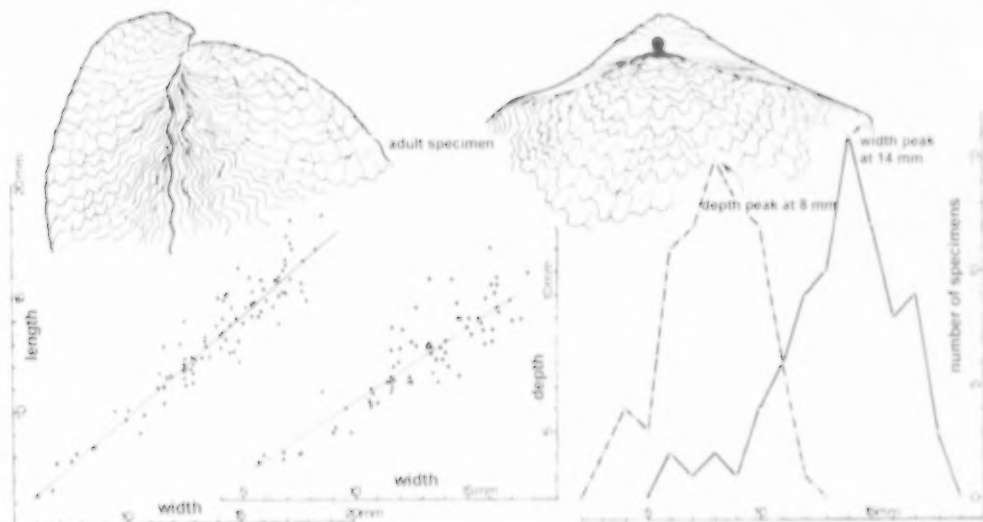
Plectatrypa mediocris Severgina 1962, Uskuchev River, Gorno Altai, Siberia, Ashgili [probably = *Eospirigerina*].

Plectatrypa (*Plectatrypa*) *imbricata* (Sowerby, 1839)
Pl. 18C, figs. a-r; Figs. 49, 50

1839 *Terebratula imbricata* Sowerby, p. 624-625, pl. 12, fig. 12 (left-hand figure only).

Type locality and horizon. 'Wenlock limestone, Wenlock Edge' (Sowerby, 1839). Cocks (1978) noted that the correct locality, as from collections, should be 'Tame Bridge, Walsall' and the horizon is the 'Much Wenlock Limestone' of the West Midlands. The original specimen figured by Sowerby (1839, pl. 12, fig. 12, left side only) could not be found in the Geological Survey collections, nor in the Natural History Museum, and is apparently lost. Bassett and Cocks (1974) selected Geological Society specimen 6600 as lectotype, but unfortunately this specimen is undoubtedly the type of *P. abbreviata* and is figured clearly by Sowerby as the specimen on pl. 13, fig. 27, even down to the small details of the number of ribs and their location on the dorsal valve (see reproduction of Sowerby figures, fig. 77). There is no mention of the type specimen of *P. abbreviata* in Cocks (1978). The Natural History Museum specimen from the Davidson collection is selected as neotype herewith (BB55347), and is labeled as coming from the 'Wenlock Shale, Walsall'. A paraneotype from Dudley (BB27099), from the same locality, also shows a similar well-preserved shell. Possibly this level refers to the equivalents of the upper Farley Member of the Coalbrookdale Formation, and would thus be within the *nassa* Zone (Bassett et al., 1975). But specimens from the 'Wenlock Limestone' elsewhere could also include strata of *deubeli-ludensis* age (Hurst et al., 1978; Bassett, 1989). Bassett (1974), in his review of Wenlock stratigraphy, and Ratcliffe (1988) analyzing facies, do not cite *Plectatrypa imbricata* from the Walsall and Dudley area, where the sequence of the Wenlock Limestone and underlying shale is about 60 m thick. The exact level of the original collection of Sowerby is thereby unknown. I have

Fig. 49. *Plectatrypa (Plectatrypa) imbricata* (Sowerby, 1839). Statistical evaluation based on pooled collections from the Walsall and Dudley areas, late Wenlock. The peaks are quite uniform, suggesting that collections are homogeneous: depth peaks at 8 mm, width peaks at 14 mm. Camera lucida drawing of adult specimen.



collected the species from shaly, nodular beds directly below the upper Wenlock limestones at Wren's Nest, and this suggests that this species is more abundant at that lower level, where *Endrea lonsdalei* also occurs. Hurst (1975) reported *P. imbricata* from the *Eoplectodonta*, *Isorthis*, and *Sphaerirhynchia* communities, but his species may also have incorporated the older *P. abbreviata* or even *Spirigerina lockwenia*.

Diagnosis. Medium-sized, averaging 14–15 mm width, strongly dorsibiconvex and rounded shells with 35–45 ribs on adult shells, and 4–6 ribs on the dorsal fold.

Description. Medium sized, average width 14–15 mm, slightly wider than long, average length 12–14 mm, average depth 7–9 mm; shell shape inflated, dorsibiconvex with prominent anterior fold; shell outline rounded laterally and anteriorly; hinge line sharply indented; hinge angle from 120° to 135°. Beak incurved; small anacline area; foramen rounded, well developed, apical to transapical in gerontic shells, bounded by small, well-defined, triangular deltidial plates. Ribs strongly developed, clearly defined, averaging about 35–40 ribs on medium-sized adult shell; on vv single rib pair at apex diverging to form enlarged rib pair normal flanking each side of the normally sharp-edged sulcus, in which are 3–5 ribs, with flanking ribs normally intercalated; dv with rounded, U-shaped to slightly angular fold covered by 4–6 ribs and flanking ribs normally bifurcating; ribs initiated on vv with single rib pair flanked by 2 lateral ribs. Imbricate growth lamellae very short, evenly and continuously spaced at about 0.3–0.5 mm; slightly deflected about 0.5 mm from shell, overlapping at anterior commissure.

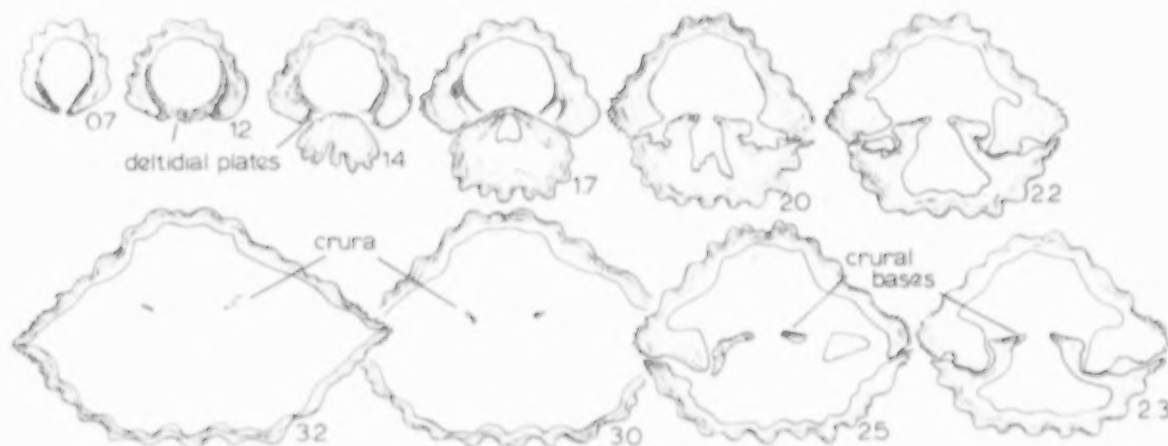
On interior of vv, distinctive, strong, partly hollow deltidial plates interlocking at contact, opening and expanding anteriorly to line interior of pedicle cavity; dental nucleus minute to insignificant apically, absent distally; giving way to crural notches opened on ventral portion of teeth; teeth blunt, short, pointing dorsomedially, with accessory lobes at

side separated by sinus. Dorsal valve with large cardinal pit, expanded into gap with moderately developed median septum; hinge plate solid; thick hinge pad underpinning thin socket plates; crural bases relatively delicate, narrow, giving rise to short, ventrolaterally directed crura. Jugal processes and spiralia not discovered in specimens sectioned.

Remarks. *P. imbricata* is 20–30% larger than *P. abbreviata* and has a more rounded profile. On the other hand it is smaller than many *P. parimbricata*, with finer ribs and more closely spaced growth lamellae. The sizable pedicle opening and position of the beak, and development of epibionts on both valves, especially anteriorly, suggest these were in a life position with the umbo close to attachment points on the substrate, and lateral commissure oblique to vertical. The common distribution of *Plectatrypa imbricata* in the Dudley 'Wenlock Limestone' suggests that the levels from which it was collected at Dudley are either within the Lower Quarried Limestone Member or slightly above that, and support the idea that the lower Dudley Limestone is older than the limestone at Wenlock Edge. Therefore, the 'Dudley' material was probably collected from equivalents of the Farley Member. At the east side of Wren's Nest, Dudley (Hardie, 1971, locality B), *Plectatrypa imbricata* was personally collected about 1 m below the upper quarried limestone level, thus suggesting that the type horizon of *P. imbricata* was probably within the upper Nodular beds. Since *Plectatrypa* is primarily a deeper water genus, this would be confirming evidence. There is no mention of the occurrence of this species at new exposures mentioned in Hamblin et al. (1978).

Materials. Total 88 specimens from the 'Wenlock Shale' or 'Wenlock Limestone' in various localities mostly to the northeast around Walsall and Dudley. **Walsall** [locus typicus], 'Wenlock Shale' and 'Wenlock Limestone', B611 [4], BB55311–28 [16], B8610 [1], B80417 [7], B138910 [8]; **Dudley**, Wenlock Lst., B23219 [1], BB55327–33 [7], BB55336–44 [8], BB55347 [1], B34780 [2], B34781 [8].

Fig. 50. *Plectatrypa* (*Plectatrypa*) *imbricata* (Sowerby, 1839). Serial section of specimen A26626, 'Wenlock Limestone, Dudley', probably from Nodular Limestone directly below Upper Quarried Limestone at Wren's Nest, late Wenlock; note loss of spiralia and jugal processes in this shell, retraction of deltidial plates well within pedicle cavity; $\times 5$.



B3919 [1], B24029 [1], B97775 [3], B12163-5 [2], B8610 [5], A26615-38 [23], A26667 [3], A2668-71 [4]; Wren's Nest, Dudley from the Farley Member, upper Coalbrookdale Formation, about 2–3 m below the Wenlock Limestone, *nassa* Zone, GB12 [8]; Br110911-3 [3]; Wenlock Edge, Wenlock Limestone, B641 [6]. The species does not occur on Gotland in the equivalent Mulde Marl or Klinteberg units.

Plectatrypa (*Plectatrypa*) *abbreviata* (Sowerby, 1839)
Pl. 19A, figs. a–z, aa; Fig. 51

1839 *Terebratulina imbricata* var. *abbreviata* Sowerby, p. 631, pl. 13, fig. 27.

Type locality and stratum. 'Wenlock Shale, Woolhope', Malvern Hills (first locality cited by Sowerby, 1839). This suggests horizons above the late Llandovery – early Wenlock Woolhope Limestone, and in the Lower Wenlock Shale (see section 66, Ziegler, Rickards, and McKerron, 1974). Squirrell and Tucker (1960, 1967) provided no information on the occurrence of this species within the Woolhope inlier, although they mentioned '*Atrypa reticularis*' and '*Glossia obovata*'. *Plectatrypa abbreviata* is quite common in the region [see Whitman's Hill Coppice below], and also in the Buildwas Formation of Shropshire. Bassett and Cocks (1974) selected the specimen of var. *abbreviata* Sowerby (1839) as type for *P. imbricata*; this is corrected herewith (below). An unsuccessful attempt was made to rediscover the type locality and to find other collections labeled as 'Woolhope'. The probable level from which this species was derived is the high *Cyrtograptus purchisoni* Zone, i.e., lower Sheinwoodian, early Wenlock. A new collection was made at Whitman's Hill Coppice [west side of the Malverns], a temporary road cut exposure along the west side of Highway A4103; this yielded 20 specimens similar to the type, from the middle to upper parts of the Wenlock Shale. This locality is not referenced in Penn (1971), nor Squirrell and Tucker (1967). The lectotype, herewith designated from the Geological Survey collection (GS6600), is clearly the speci-

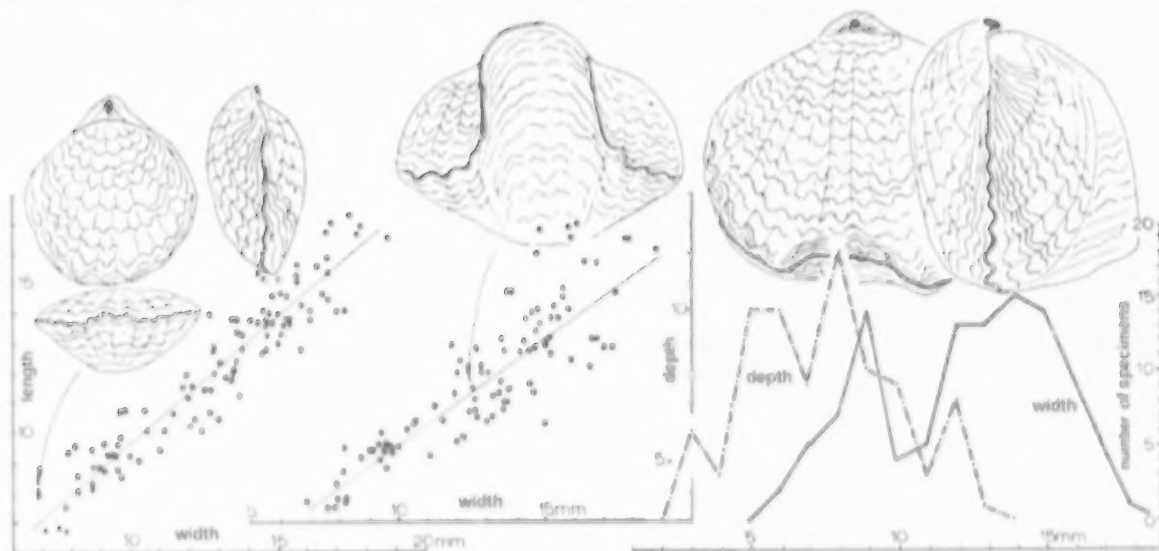
men figured by Sowerby (it has exactly the same number of ribs, anterior fold, and shell morphology; examination of the lectotype by transparent overlay of the Sowerby figure shows an exact match). On Gotland, this species is common in the Upper Visby beds, particularly in peri-reefal facies of the Axelro Mbr., i.e., within the *murchisoni* Zone, and ranges through Höglint strata, of *riccartonensis* age. I have no information on whether *P. abbreviata* occurs in the earliest Wenlock Woolhope Limestone (see Ziegler et al., 1974), e.g., the age equivalent of the Upper Visby beds on Gotland, where the species is common.

Diagnosis. Relatively small to medium sized (12–15 mm wide), globose *Plectatrypa* with narrow dorsal fold covered by only 2–3 ribs.

Description. Rounded, globose, dorsibiconvex; maximum width near mid-length; average widths 12–15 mm (maximum 18 mm), slightly wider than long as adult shells, but longer than wide, biconvex in early growth stages; average depths 5–8 mm (maximum 13 mm). Hinge line slightly indented, rounded; hinge angles about 120°–130°, narrower in neanic stages; rounded hinge corners. Beak small, blunt; anacline to almost hypercline area in adult shells, orthocline in neanic stages; adult foramen nearly always transapical, penetrating well into umbo. Anterior commissure strongly U-shaped in adult shells, but weak to nearly rectimarginate in neanic shells; ribs poorly developed on sides of dorsal fold, which may be nearly smooth; growth lamellae short, spaced at less than 0.4 mm, imbricate, somewhat deflected away from the shell surface, almost developed into small caps on the crests of ribs; ribs numbering about 24–30 on adult shells; ventral carination produced by strong mid-rib pair diverging and bifurcating anteriorly; dorsal fold covered by 2, less commonly 4 ribs.

Remarks. This species is usually a rare faunal component, sometimes common, but never abundant and bed-forming. No serial sections were made. Specimens differ from the type species *P. imbricata* and *P. parimbricata* n. sp. in being smaller, with finer ribs and with fewer ribs covering the dorsal

Fig. 51. *Plectatrypa* (*Plectatrypa*) *abbreviata* (Sowerby, 1839). Statistical evaluation of specimens pooled from Buildwas localities, early Wenlock; camera lucida drawings of neanic, adult specimens. Note that neanic specimens show little fold development.



sulcus, which is relatively low and weak in many specimens. The few specimens from the Upper Visby beds tend to be somewhat smaller than the specimens from the Malverns: in addition the Upper Visby forms have less accentuated rib imbrication. On the other hand, shells from the Högkint beds show morphologies close to the British form of *P. abbreviata*, and are here thought to belong to the same species.

Materials. Total 107 specimens. British specimens derive from the 'Wenlock Shale' and Buildwas Formation at various localities stretching from the Malverns through Shropshire. The Whitman's Hill Coppice collections are not far from Woolhope, the type locality. **Crabtree Corner**, B10089 [3], B10090 [1]; **Walsall**, A26643 [1], B38702-3 [5]; **Buildwas**, B27879 [2], B20798 [3], B27099 [3], B61057-8 [2]; **Whitman's Hill Coppice**, lowermost shales in roadcut A4103, Malverns, 744:483, GB13c [20]; **Malverns**, Wenlock Shale, B3244 [6]; **Colwall**, B10106 [1], B10108 [1]; **Barr**, Staffordshire, B12127 [2], Br12122-4 [3]; **Garcoed**, Wales, B3310 [1], B3563 [1]; **Moel-y-garth**, Welshpool, B12125-6 [2]. Gotland specimens come from Upper Visby beds to Högkint beds, with material from the Högkint beds being most similar to the British materials. **Upper Visby beds**: **Snäckgårdet**, Visby, Br122572-81 [10], Br47388 [1], Br121782 [1]; **Snäckgårdsbaden**, Visby, Br107505 [1], Br107972 [1]; **Visby 'b'**, Br41791 [1]; **Kopparsvik**, Visby, Br131279-81 [3]; **Gnåsvärd I**, Tofta sn., Br10900-02 [3], Br134552-3 [2]; **Gnåsvärdshamn**, Br108086 [1]. **Högkint beds**: **Ringvide**, Väske sn., Br123264-66 [3]; **Stranden vid Ringvide**, Väske sn., Br103423 [1]; **Klinter NO Stenkyrkehuk**, Br123615 [1], Br121777-78 [2]; **Storbrut**, Stenkyrke sn., Br10907-10 [4]; **Körpkint**, Västerhejde, Br10903-05 [3], Br103420-22 [3], Br103407 [1]; **Häftingsklint**, Hangvar sn., Br121779 [1], Br107968-71 [4], Br102694-6 [3], Br55283 [1]; **Galgbacken**, Visby, Br115553-4 [2]; **Stuguklint**, Stenkyrke sn., Br107943 [1], Br107941-43 [3]; **Bogeklint**, Boge sn., Br105839-40 [2].

Plectatrypa (*Plectatrypa*) *parimbricata* n. sp.

Pl. 16C, figs. k-n; Pl. 19B, figs. a-j, o-s; Figs. 52-54

1861 ?*Atrypa marginalis* var., Roemer, p. 47-48, pl. 5, figs. 13a-b ['Sadewitz', glacial erratics, N Germany].

1885 *Atrypa marginalis*, Roemer, p. 67, pl. 4, figs. 7a-b (same as above).

1930 *Plectatrypa imbricata*, Schuchert and Cooper, pl. 2, figs. 16-21 (Schuchert colln., 'Silurian, Gotland').

Type locality and stratum. **Lerberget I**, locus typicus [= Lushälet I], Stora Karlsö Island, off W coast of Gotland. The designated type locality is a bluff directly below the panoramic lookout at the lighthouse near Lerberget, probably the same collecting locality as Lushälet I, which is designated here the 'locus typicus restrictus', at Stora Karlsö, 61 Visby SO 53550:29800 (= SW112). The type horizon is the uppermost Slite beds, particularly the more abundant horizon exposed in the bluff along the coast, about 3-5 m below the medium-thick bedded, resistant weathering limestones that make up the lower part of the 'Klinterberg' facies at Stora Karlsö, NW side. *Plectatrypa* is apparently absent in the Mulde Marl, which has a rich *Oglupes muldea* fauna in almost identical sediments. The *Plectatrypa* shales from Karlsö are presumed to lie stratigraphically below the Mulde Marl. This suggests that the species occurs within unit 'G' of the Slite beds (sensu Laufeld and Jeppsson, 1976). This level possibly lies within the *ellesae* to as high as the lower *lundgreni* zones, upper Sheinwoodian - lower Homerian (mid-Wenlock). The species occurs abundantly in soft-weathering shales directly below a 20-30 cm thick resistant calcarenite ledge, in turn below the 1-3 m thick beds typified by the very large rugose solitary coral *Dokophyllum* ['*Omphyma*' in the older literature]. In some places along the bedding plane, *Plectatrypa* occurs in biostromal thickets of thin, slender, phaceloid rugosans, with *Septatrypa karlsoa* n. sp., suggesting the possibility that it

Fig. 52. *Plectatrypa (Plectatrypa) parimbricata* n. sp. Statistical evaluation of specimens from the Stora Karlsö outcrops of the Slite beds, from the coral biostrome layer, <50 cm thick, representing single bedding unit; middle Wenlock.

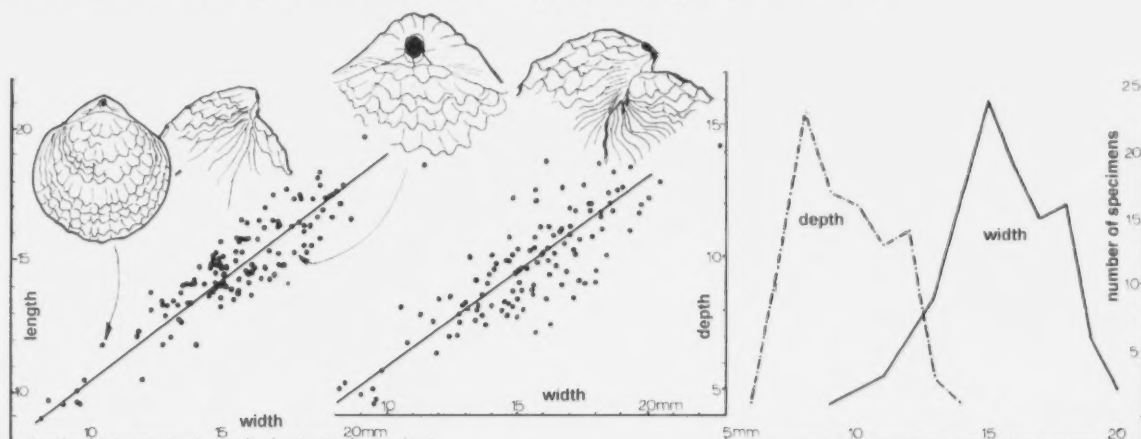
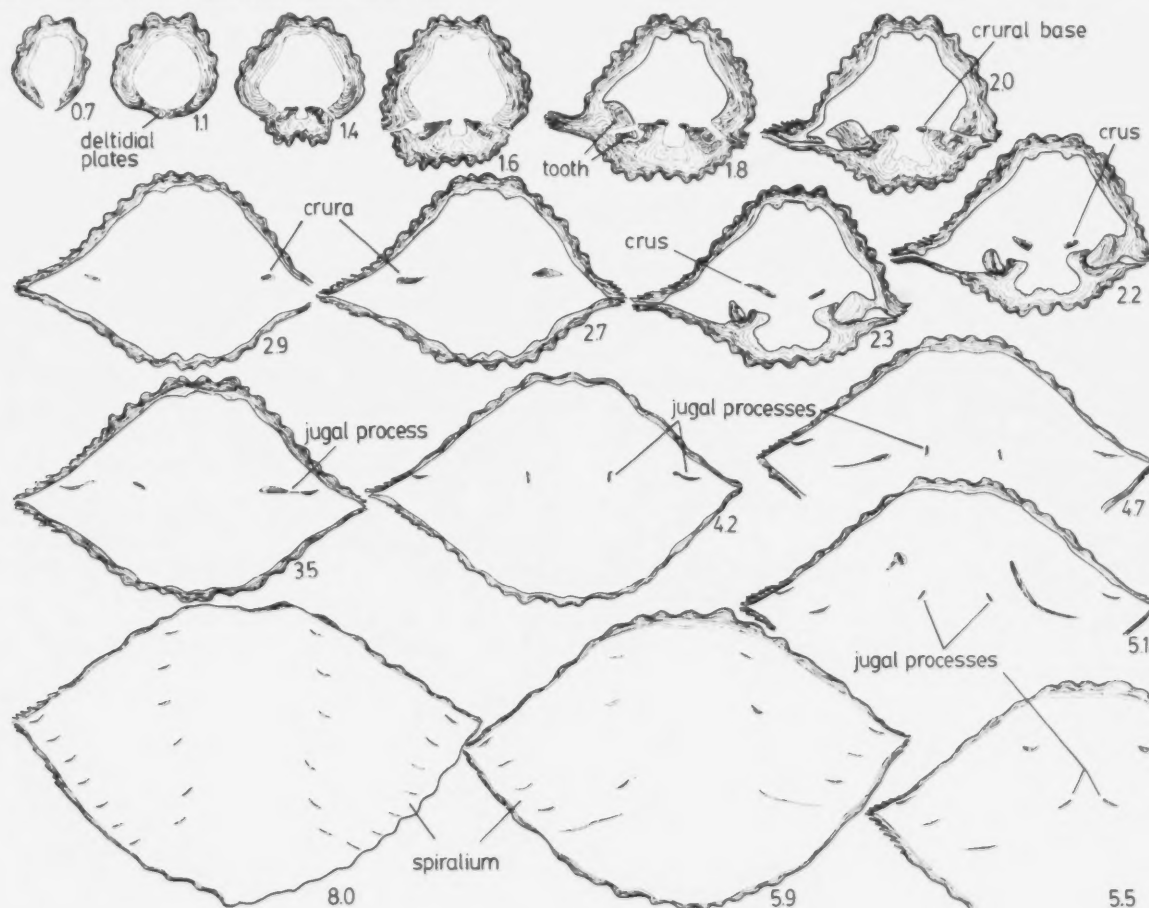


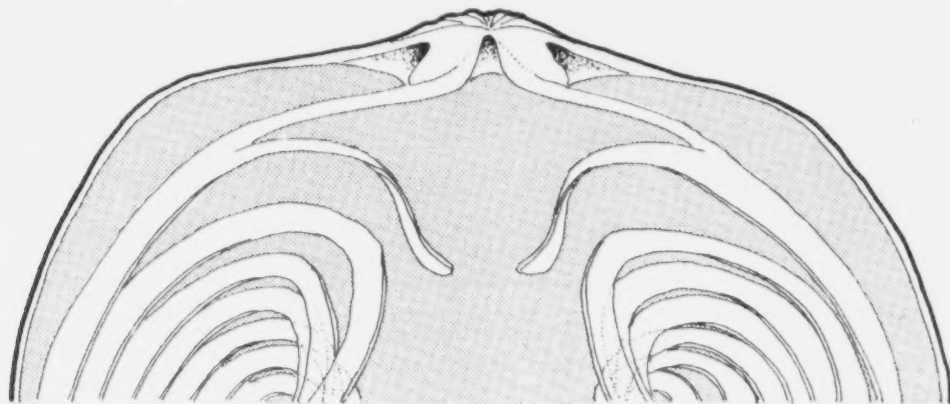
Fig. 53. *Plectatrypa (Plectatrypa) parimbricata* n. sp. Serial sections of specimen from Hien 1, N shore of Stora Karlsö, Slite beds, middle Wenlock. Note delicate crura, thin shell; $\times 4$.



was living between these corals or attached to them. Near Västergarn, on Gotland, it occurs in soft-weathering shales without associated corals. Samtleben et al. (2000) place the

Västergarn outcrops in their distal shelf carbonate facies, but on Stora Karlsö there is local shallowing and reef development in the upper Slite facies.

Fig. 54. *Plectatrypa* (*Plectatrypa*) *parimbricata* n. sp. Reconstruction from serial sections of specimen from Hien 1, N shore of Stora Karlsö, upper Slite beds, middle Wenlock (as in previous figure); $\times 8$.



Diagnosis. Relatively large *Plectatrypa*, averaging 15–18 mm in width, strong, U-shaped, sharp-edged, dorsal fold, covered by 4–6 ribs.

Description. Wider than long shells, maximum width about 21 mm, averaging 15–18 mm, young shells equidimensional, depths averaging 8 mm (maximum depth 14 mm); shells rounded in early stages, changing to subrounded later, with relatively straight or only weakly indented hinge; well-rounded hinge corners; apical angles 125° – 130° ; anterior fold normally well-rounded, highly arched, sometimes lacking distinct margins; ventral sulcus clearly delimited in most shells by diverging rib pairs, with sulcus occupied by 3–5 ribs; ribs fairly even, stronger along ventral side to produce carination by diverging mid-rib pairs; up to about 35 ribs per valve; ribs intersected by regular, short growth lamellae, short, spaced at 1 mm, more crowded along anterior commissure hugging shell surface; beak prominent, somewhat pointed; anacoline area in adult shells, orthocline in neanic forms; umbo normally penetrated by relatively large, prominent, rounded, expanding transapical foramen, flanked by small deltidial plates. Internally, small, hollow deltidial plates lining delthyrium, but not extending into the vacant pedicle cavity. Teeth, solid, short, lacking dental cavities, but with small, offset dental nuclei along inner shell wall margin, or no nuclei; crural notch anteriorly. In dv, hinge plate fortified by hinge pad; socket plates thin, horizontal, giving rise to relatively delicate crural bases and crura, diverging laterally; jugal processes thin, delicate, extending to middle but distant, recurved laterally at middle; fewer than 7 spiral whorls, relatively widely spaced, dorsally directed.

Remarks. Schuchert and Cooper (1930) used this species to illustrate and define their genus *Plectatrypa*, but designated *Plectatrypa imbricata* as type species. This species is larger than either *P. abbreviata* or *P. imbricata*, and with fewer, coarser ribs per unit shell width for those shells of the same size. It is the largest *Plectatrypa* species in the region. Marr and Nicholson (1888) described *P. flexuosa* from the early Llandovery Skelgill Shales of Britain, which is even larger (>20 mm wide) but probably assignable to the plectatrypine genus *Sypharotrypa*. *P. parimbricata* appears to be absent in England, and is thus difficult to compare directly, but a few

specimens from the Girvan region of Scotland are tentatively assigned here. Specimens of this larger species appear also to have been discovered in glacial erratics at Sadewitz, northern Germany (Roemer, 1861, 1885).

Materials. All 255 specimens come from the upper Slite beds of Gotland, primarily from the west coast of Gotland, and Stora Karlsö. **Lushälet 1** [probably = Lerberget 1 from old collections], bluff directly below panoramic lookout at light-house, Stora Karlsö, 53550:29800, SW112 [10]; **Lerberget 1** (type locality), Stora Karlsö [the precise collecting locality here is unknown, but the localities around Lerberget, here called **Ramroir**, **Lerberget**, and **Lushälet 1**, all produced *Plectatrypa* from the 'beet reef', solitary coral biostromes]. On Gotland the species is found in the Slite beds from around Västergarn. **Lerberget 1**, Br41647-70 [24], Br112329-58 [30], Br123226-30 [5], Br103953-4 [2], Br108058 [1]; **Lerberget 4**, small sloping bluff along coast directly N of slumped rock unit, Stora Karlsö SW111 [3]; shoreline outcrop at **Hien 1**, Stora Karlsö [28]; **Hien 1**, shaly units interbedded with *Dokophyllum* (= '*Omphyma*') beds, Stora Karlsö N coast SW108 [5]; **Ramroir 1**, base of seabuff with bedding plane outcrops, SW109 [1]; **Ramroir 2**, coastal bluff W side Stora Karlsö, shaly units at base of bluff, SW110 [9]; **Barabacke**, Hörsne sn., Br41908 [1]; **Västergarn**, Br121781 [1], Br41868-907 [39], Br41849-67 [19], Br110911-40 [30]; S om **Västergarnshamn**, Br108040-45 [6]; **Kanalen 1.8 km an Västergarn**, Sanda sn., Br108059-61 [3]; **Valbytte 1**, Sanda sn., Br123491 [1], Br134038-41 [4]; **Stranden S om Valbytte fisklage**, Br107879-81 [3]; **Lilla Karlsö**, ?Br61111 [1]; **Idå 1**, Västergarn sn. [3, not catalogued]; ditch outcrop 200 m S of **Lekarve 1**, S of Västergarn, SW13 [2]; **Valbytte 6**, ditch outcrop, 68580: 40920, SW14 [19]; **Valbytte 7**, ditch outcrop 100 m S of Lekarve 1, 68480:40920, SW15 [6]. In Britain at **Woodland Point, Girvan**, Saughill Group, A34984-7 [4 broken shells].

Plectatrypa (*Gutnia*) Copper, 1996b

Type species. *Plectatrypa* (*Gutnia*) *capidula* Copper, 1996b, Tjälädersholm, upper Slite beds, middle Wenlock.

Range and distribution. Late Llandovery–Ludlow.

Diagnosis. *Plectatrypa* with very fine, evenly sized ribs (8–10 per 5 mm), lacking distinct ventral mid-rib carination, concentric growth lamellae expanded into short, blunt-ended, pseudo-spines each of which forms a cap-like crest (capidula).

Remarks. *Gutnia* resembles finely ribbed *Plectatrypa* that lack the sharp and distinct ventral double carination and dorsal fold, and in which ribs are not enlarged, but evenly sized over the shell surface. *Gutnia* has capidulate ornamentation, the result of small caps at the end of each growth lamella – rib intersection. Internally, it has small dental nuclei instead of solid teeth, a feature probably derived neotenously from *Plectatrypa*, as adult *Plectatrypa* appear to lack recognizable dental nuclei and have no dental cavities. This species is thus far not identified from British museum collections, but Parkinson (1833) illustrated a homeomorph from an unknown locality and horizon: whether this is a Silurian brachiopod is doubtful. Buch (1835, p. 79–80) related this to the Linnaeus species *Atrypa reticularis*, but then also cited its source as British Jurassic localities from Bath and Wiltshire, and French localities of Calvados, and Caen [these may refer to the Jurassic rhynchonellide *Acanthothyris*]. Thus Buch had a very different view of the nature of Silurian species and did not accept Dalman's view (1828) of the genus *Atrypa*, stating that it was a 'doppelte Namen für schon vorher benannte Formen' [a duplicate name for previously named forms]. The very fine ribs of *Gutnia* suggests it may have given rise to the Atrypinellinae via the genus *Reticulatrypa*, and ultimately to the Punctatrypinae in the Devonian.

Species assigned.

Plectatrypa (Gutnia) capidula Copper, 1996b, Gotland, upper Slite beds, Wenlock.

?*Terebratulites coarctatus* Parkinson 1833 (nomen oblitum), horizon unknown, possibly Dudley, late Wenlock? [cited by Buch, 1835, as Silurian; possibly Jurassic rhynchonellide].

?*Plectatrypa arctoimbricata* Amsden 1968, Searcy County, Arkansas, St Clair limestone, Ludlow.

Specimens illustrated as '*Plectatrypa imbricata*' and *Plectatrypa* sp. by Nikiforova (1961) from the late Llandovery of Siberia are very similar and possibly assignable to this subgenus.

Plectatrypa (Gutnia) capidula Copper, 1996b
Pl. 20A, figs. a–m; Figs. 55, 56

1833 ?*Terebratulites coarctatus* Parkinson, p. 229, pl. 16, fig. 5 [source locality unknown: see Buch, 1835].

1996b *Plectatrypa (Gutnia) capidula* Copper, p. 915, 917, fig. 1.

2002b *Plectatrypa (Gutnia) capidula* Copper, p. 1428, fig. 967-2.

Type locality and stratum. **Tjälderholm 1**, Boge parish, eastern Gotland, small shoreline outcrops with bedding plane surfaces exposed, about 80–100 m southeast of small jetty, 6J Roma NV 93630:77400 [corrected from Copper, 1996b]. Shaly, 10–20 cm thick unit of thinly bedded calcarenites exposed directly below 2–3 m thick, small coral patch reefs dominated by *Acervularia*. Specimens are found in clusters and isolated shaly pockets, especially best exposed at low tide. This represents a localized, shallow, proximal shelf, reef facies on the east side of Gotland. The type horizon lies in the upper few metres of the Slite beds in its eastern facies (probably unit 'G' of Laufeld and Jeppsson 1976; Jeppsson 1983); late Wenlock, Homerian, probably high *lundgreni* Zone equivalent. This may be younger than *Plectatrypa (Plectatrypa) parimbricata* from Stora Karlsö and Västergarn. Laufeld's list of localities (1974) cited 'Tjälderholm 1', but there is no mention here of any reefs, nor are reefs evident in Fig. 24, a photograph of this locality taken from the east side, probably further east from the collecting locality here called Tjälderholm, and the reefs.

Fig. 55. *Plectatrypa (Gutnia) capidula* Copper, 1996b. Statistical comparison of all available specimens from Tjälderholm 1, Slite beds, middle Wenlock; camera lucida view detailing ventral beak.

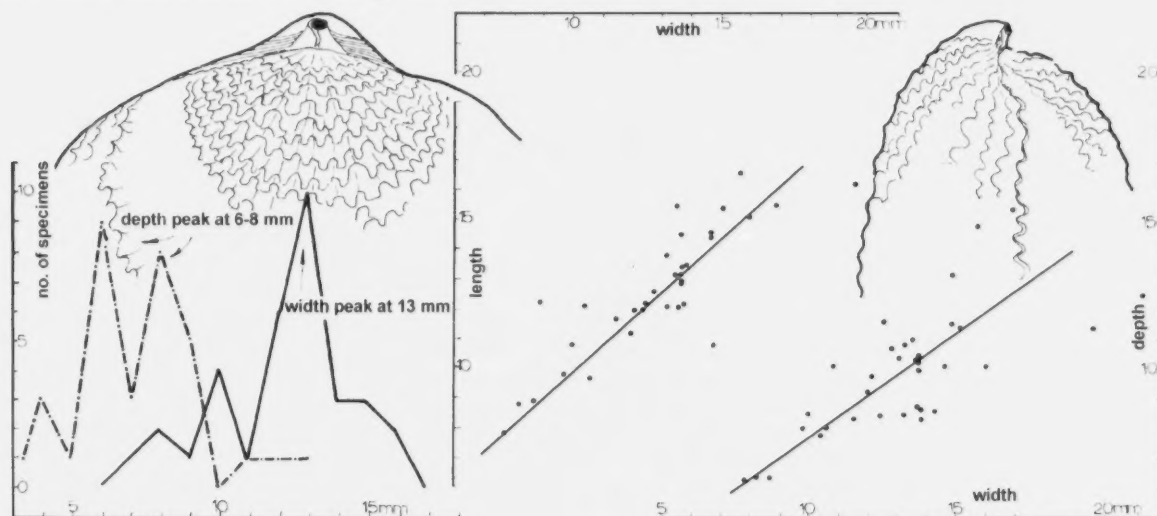
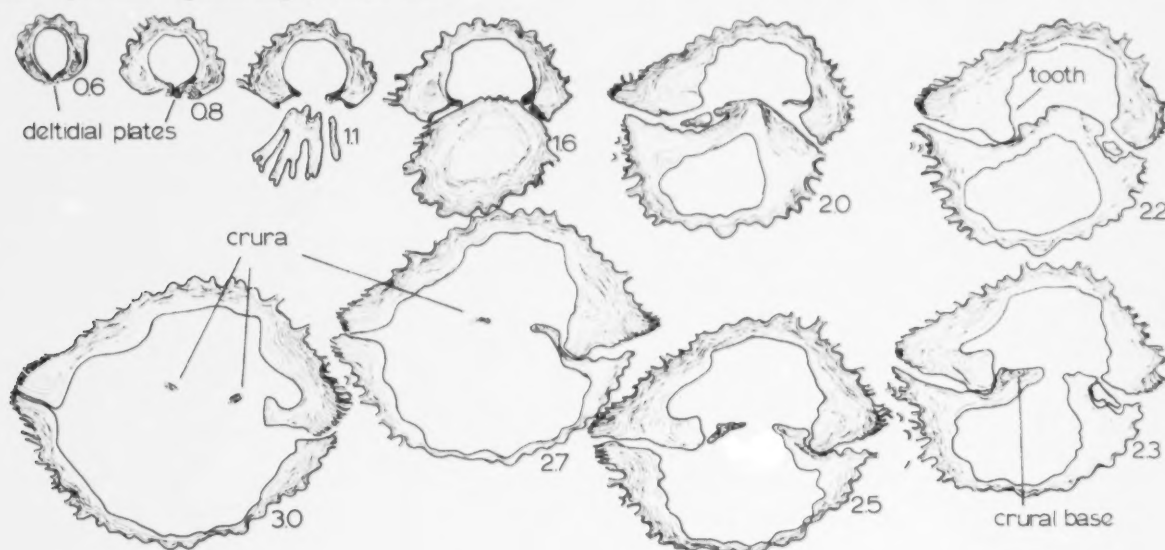


Fig. 56. *Plectatrypa* (*Gutnia*) *capidula* Copper, 1996b. Serial sections of specimen lacking spiralia and jugal processes, specimen Br105796, Tjälderholm 1, middle Wenlock; $\times 5$. Note that deltidial plates are not retracted within the pedicle cavity, small dental nucleus only in earliest growth stages, delicate crura.



Diagnosis. Small to medium-sized (maximum 14 mm width), rounded shells with very weak carination, or almost non-carinate; close, evenly spaced, imbricate growth lamellae.

Description. Medium sized, equibiconvex to weakly dorsibiconvex; averaging 12–14 mm wide, slightly wider than long, 6–9 mm deep; rounded in outline, hinge angle 130° – 150° ; hinge corners rounded and poorly defined; beak small, protruding; area orthocline to slightly anacline, exposing small delthyrium; apical to slightly transapical foramen surrounded by minute deltidial plates; ribs evenly spaced at about 9–10 per 5 mm; imbricate growth lamellae about 1 mm apart, regularly spaced from back to front, forming small caps (capidulae), short and blunt-ended (on well-preserved shells); anterior commissure weakly plicate, rounded in most shells, rarely V-shaped or angular. Internally, small anteriorly hollow deltidial plates; apical foramen; teeth solid except for small dental nucleus, expanding to crural notches anteriorly; crural bases small; crura delicate; hinge plates thin; dorsal septum weak. Spiralia and jugal processes not found preserved.

Remarks. There are few species with which to compare. The illustrated specimen of *Plectatrypa arctoimbricata* (Amsden, 1968) from Arkansas is approximately the same size as the Gotland species, but ribs appear to be even finer. The main distribution of this species is in the reefal facies of the east coast of Gotland, south of Slite. It is relatively rare on Stora Karlsö, and easily differentiated from co-occurring *Plectatrypa parimbricata*.

Materials. Total 55 specimens. **Tjälderholm 1**, Boge parish, shoreline bedding plane surfaces, type horizon in thin shaly layers below small bioherms, SW48 [21]; **Tjälderholm**, Boge sn., upper Slite beds, Br46461-2 [2], Br105785-6 [2], Br105790-96 [7]; **Solnklint**, Othem parish, Slite beds, Br105862 [1], Br134554 [1]; **Tjelders**, Boge sn., Br48859-

60 [2]; **Bogeklint**, NE end, reef limestones of Slite beds, Br105849-54 [6]; **Stora Karlsö**, Slite beds, Br41711-720 [11], Br58113, Br58115 [2]; **Lerberget 1**, Stora Karlsö, Br41635 [1]; **Lanaberget**, Othem sn., Br124109 [1]; Kanale i Martebo myr nära **Hammars**, Lokrume sn., Slite beds, Br48098 [1].

Xanthea Copper, 1996b

Type species. *Spirigerina imbricata* var. *lamellosa* Lindström 1861, Wenlock, Sweden.

Range and distribution. Wenlock; Gotland, Britain, eastern Baltic, North America.

Diagnosis. Biconvex–dorsibiconvex, small to medium sized; coarsely ribbed, coarsely lamellose; prominent carination due to ventral keel, sharp anterior fold; zigzag micro-ornament on outer surface of growth lamellae, ridge-like micro-ornament on under surface; short, blunt-ended spine-like structures terminating growth lamellae; transapical foramen; prominent, large deltidial plates fastened to inside of pedicle cavity; incurved beak; short, thick teeth with minute dental nuclei (no cavities); crura curved; jugal processes hook-like, ending in laterally directed jugal plates; spiralia dorso-medial, 5–7 whorls, calcite fibres thickened strongly on inner whorl margins.

Remarks. This genus is similar in the nature of its early stage growth in ribs, lamellae, keel, and fold to *Atrypa*, from which it differs in its micro-ornament, growth lamellae, lack of a strong ventral keel, much larger size, and very large deltidial plates lining the inside of the pedicle cavity. *Xanthea* has a zigzag micro-ornament on the outer and inner surfaces of the growth lamellae unknown in any other atrypoid shells except some *Eospinatrypa* from Gotland (Fig. 93). It shares a broadly similar overall morphology to *Plect-*

atrypa, to which it has been assigned in the past. However, the ribs of *Plectatrypa* are much finer (about twice as crowded), and the growth lamellae of *Plectatrypa* are more closely and rhythmically imbricate and more sharply up-turned at the breaking edge. *Xanthea* is broadly intermediate in morphology between *Atrypina* and *Plectatrypa*, but on the basis of its early growth stages and its internal structure, it is probably closer to *Atrypina*. Nevertheless, its affinities lie with *Plectatrypinae*, rather than *Atrypinae*.

Xanthea also shares some similarities to *Endrea* in its early rib development, but *Endrea* has ribs projected as tubular frills that have a distinctive, and different, fine ornament, and *Xanthea* lacks a broad anterior fold (its fold is made by its ventral carination). For this reason *Endrea* has been assigned to the *Atrypinae* rather than *Atrypinae*. *Eospinatrypa* Copper 1973 have ribs which bear a strong similarity to those seen in *Xanthea*, but internally both of those have lateral dental cavities and small or variably developed deltidial plates, usually incurved beaks, and the same external micro-ornament. *Xanthea* lacks the spines seen in *Spinatrypa*, and has short growth lamellae with unique micro-ornament instead. However, the rib structure of *Xanthea* shells that are poorly preserved suggest the likelihood that *Eospinatrypa* evolved from it. *Xanthea* appears to define a short-lived, Wenlock transitional species-group on Gotland and in Britain, was probably derived from *Plectatrypa*, and gave rise to *Eospinatrypa*. The youngest species of the genus is similar to specimens of *Eospinatrypa*. Its evolution demonstrates that the *Atrypinae*, *Plectatrypinae*, and *Spinatrypinae* in the Wenlock are related, and represent the branching evolution or radiation of the groups.

Species assigned.

?*Carinatina crinata* Hou and Zhao 1976a, Bateobao, Inner Mongolia, Xibiehe Fm., Ludlow.

?*Camarotoechia* (?) *pseudobidentata* Rybnikova 1967, Latvia, Wenlock.

Spirigerina imbricata var. *lamellosa* Lindström 1861, Lansa, lower Slite beds, early-middle Wenlock.

Xanthea scabiosa n. sp., Kneippbyn, Upper Visby beds, early Wenlock.

Xanthea haruspex n. sp., middle Slite beds, middle Wenlock.

Xanthea lamellosa (Lindström, 1861)

Pl. 20B, figs. n–s; Figs. 57–59

1861 *Spirigerina imbricata* var. *lamellosa* Lindström, p. 363. Hedström (1910, p. 1483), and others, have attributed this species to Löven, as also seen in museum collections. Löven's work was not published.

1890 ?*Atrypa imbricata* Sowerby 1839, Gagel, pl. 1, figs. 33a–b (glacial erratics, north Holland).

1970 *Plectatrypa* sp., Rubel, p. 33, pl. 16, figs. 1–6.

1974 *Plectatrypa lamellosa*, Bassett and Cocks, p. 30, pl. 8, figs. 7–11.

1990 *Plectatrypa lamellosa*, Bassett, p. 255, fig. 9G.

1996b *Xanthea lamellosa*, Copper, p. 917–918, fig. 3.

2002b *Xanthea lamellosa*, Copper, p. 1430, fig. 969.

Type locality and stratum. '... forekommer vid Wisby och Lansa' (Lindström, 1861). The old collections identify the shoreline of Färö, north of Lansa, as the most common collecting locality, and this locality is still identifiable today, e.g., as 'Lansa fiskläge'; or 'Lansa sjöbodan' (Jaanusson, 1986). Hede (1925, pl. 4) initially identified these strata on the map at Färö as 'Tofta-kalksten'. Judging from the collecting localities Stutsviken 2 and 3, *Xanthea lamellosa* probably comes from the lower few metres of the reefal Slite beds in its northeastern facies, a 4 m thick unit labeled unit 'A' by Hede (1960, p. 49), but identified as 'member C' in Jaanusson (1986). Stutsviken 2 could be regarded as a *locus typicus restrictus*, as the location is precisely marked. These Lansa strata were called lower Slite beds by Bassett and Cocks (1974) and marked as the type horizon. The level

Fig. 57. *Xanthea lamellosa* (Lindström, 1861). Statistical variation for cumulative localities from the lower Slite beds, Färö, combined from Stutsviken 2, 3, and the Lansa, Färö localities, early Wenlock; width peak at 15–18 mm, depth at 8 mm. Detail of beak from typical shell, ca. $\times 6$.

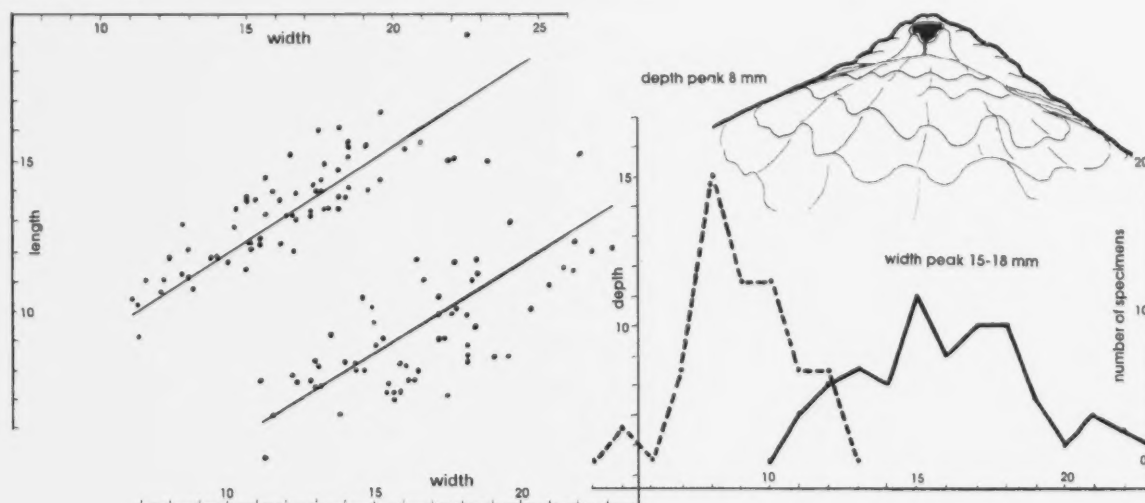
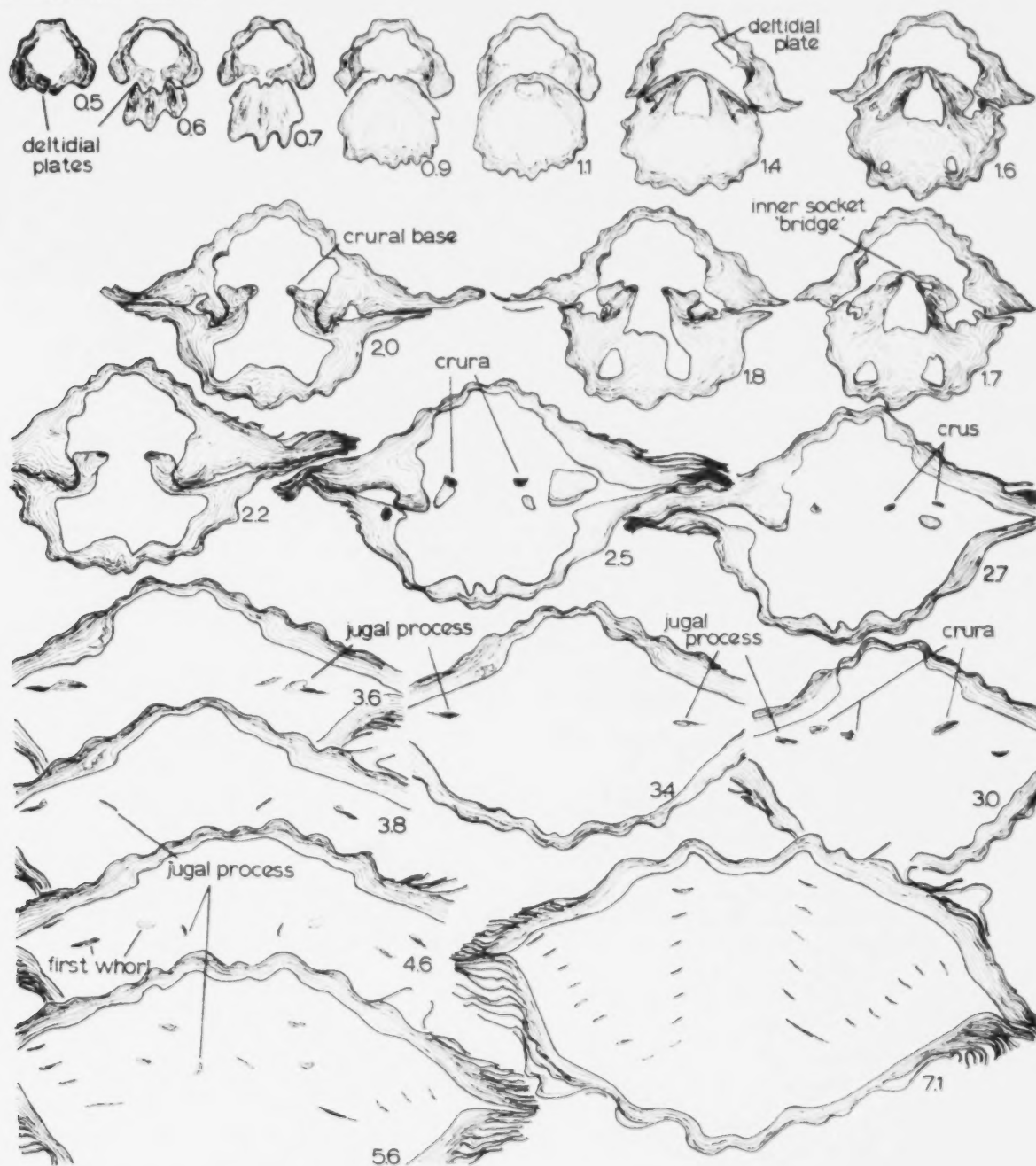


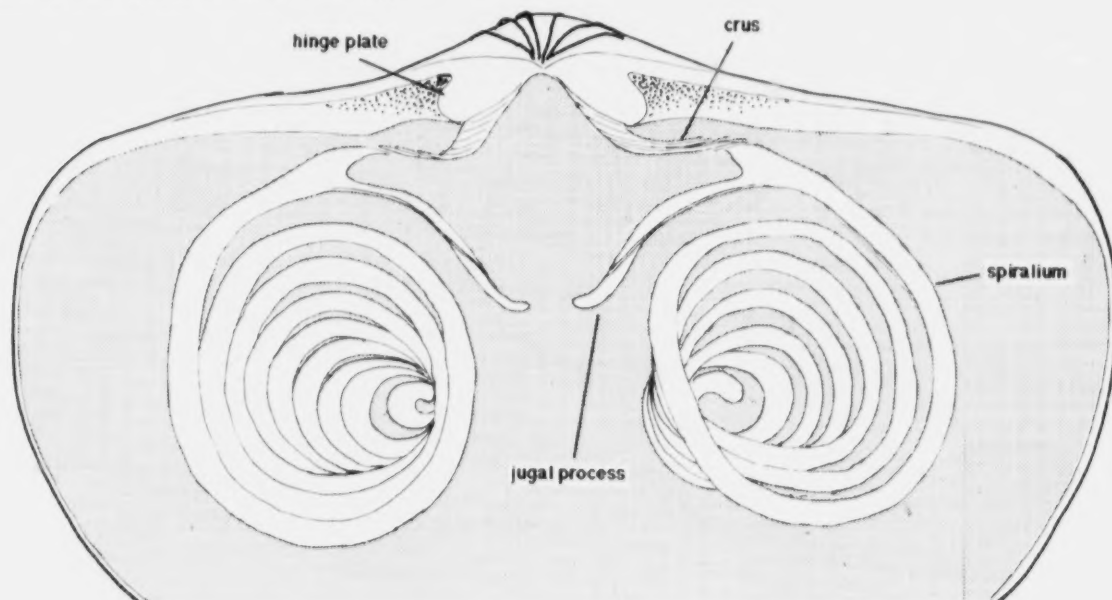
Fig. 58. *Xanthea lamellosa* (Lindström, 1861). Serial sections of hypotype Br104014, 'viken NV om Lansa, Färö', lowermost Slite beds, early Wenlock. Note the prominent, wide overlapping growth lamellae, unusual inner socket ridges bridging the notothyrial pit, incurved jugal processes, $\times 5$.



from which this species is derived appears to be set in the *rigidus-limmarsoni* zones, middle Sheinwoodian. Bassett and Cocks (1974) also believed the species occurred as low as the Upper Visby beds, but in this revision these specimens are assigned to a different species, *X. scabiosa*. *X. lamellosa* may range down into the 'Tofta Limestone' or the uppermost Höglint beds, i.e., the Kopparsvik Formation of Rid-

ing and Watts (1991), who make no mention of this species. The sedimentary facies of the Kopparsvik Formation contains no reefs, but the Gütevågen and Visborg members are biostromal and contain stromatoporoids, bryozoans, and corals; other members are less likely to contain *Xanthea*. It is uncertain if some old collections labeled 'Höglint' could in fact refer to Kopparsvik Formation faunas. A disconformity

Fig. 59. *Xanthea lamellosa* (Lindström, 1861). Reconstruction from serial sections, Br104014, Lansa, Färö, early Wenlock, demonstrating relatively small spiralia in dorsal shell cavity, $\times 10$.



is said to separate the Kopparsvik from the lower Slite Formation (Riding and Watts, 1991), and the reefs of the lowermost Slite at Lansa on Färö Island could be built on this foundation. The possibility cannot be excluded that the lowermost reefs of the Slite, containing *X. lamellosa*, could be stratigraphic equivalents of the upper Kopparsvik Formation. The setting is a proximal shelf, shallow reef facies, co-occurring with *Endrea*, rhynchonellids (?*Stegerhynchus*), and corals.

Diagnosis. Relatively large, deep, wide, dorsibiconvex *Xanthea*, with widths 17–22 mm, lengths 13–16 mm, depths 10–12 mm, large beak, prominent foramen, deltidial plates, coarse ribs, few growth lamellae.

Description. Large, considerably wider than long, thick, dorsibiconvex shells; averaging 15–18 mm wide, 7–10 mm deep; prominent, squared anterior fold. Ventral beak large, protruding above dv by 1–2.5 mm; area usually apsaeline; adult foramen commonly transapical, large, open, with expanded deltidial plates; ribs coarse, ca. 3 per 5 mm, ventral mid-rib pair raised, diverging, with 1–3 small ribs in depression; dorsal valve with relatively evenly spaced ribs, ca. 10–11 per valve surface; growth lamellae prominent, overlapping at commissure, spaced at >2 mm in apical to central part of shell; special micro-ornament located on underside of growth lamellae (in detailed peel sections). Interior of vv with thick, prominent deltidial plates interlocked medially, opening into groove anteriorly, lining the inside of the pedicle cavity; teeth thick, solid, lacking dental nuclei, with weak lateral lobes; dv with large cardinal pit; weak, low cardinal process; prominent dorsal septum; inner socket ridges bridged by unusual capping structure; hinge plate moderately thick; large inner socket ridge, weak middle socket ridge; crural bases small, projected laterally as curved, unfeathered crura; jugal processes horizontal, with thick bulging growth, curved dorsocentrally to end in thin, laterally

directed jugal plates; spiralia 5–7 whorls, thickened strongly on the inner margins, dorsomedially directed.

Remarks. *Xanthea lamellosa* (Lindström, 1861) is distinguished from its predecessor species *X. scabiosa* in its larger size, much wider than long shell, more inflated dorsal valve, and larger foramen, area, and beak. Bassett and Cocks (1974) pooled the specimens from the Upper Visby through Slite beds into one species, but a finer subdivision is used here. *Xanthea lamellosa* is prominent in reefal, coral-rich parts of the lower Slite beds in its northeastern facies, co-occurring, and about equally abundant as *Endrea echoica*. Rare specimens from the Höglint beds approach the size of the Slite species, and the two species may intergrade morphologically. A single specimen is labeled as 'Stora Karlsö', but the horizon is unknown.

Materials. Total 149 specimens from the Slite beds. **Lansa, Färö**, locus typicus, Br102582–89 [6], with remaining specimens figured by Bassett and Cocks (1974), Br41623–32 [10], Br41725–40 [16]; '**Färö, viken NV om Lansa**', Br104012–14 [3]; **Stutsviken Fiskestuga**, loose shells from beach ridge 50 m W of Fiskestuga, 1 km N Lansa, 90–51G 37–54 [18]; **Visby**, east Visby 1, "dike vid landsvägen till Endre circa 1250 m fra Österport", Br103872–77 [6 spec.]; **Käringen 1**, Visby sn., Br124801–4 [4]; **Stora Karlsö**, Br42343 [1]; **Stora Myre**, Martebo sn., Br46910–36 [27], uncatalogued 3 specimens; **Martebo trask**, Martebo sn., Br43449 [1], Br43451 [1]; **Föllingbö** sn., Br47282 [1]; Runes, Martebo sn., Br48094 [1], Br43347 [1]; kanal nära **Hammar** i Lokrume, Martebo sn., Br47296–306 [6]; **Lokrume kanal**, Lokrume sn., Br62741–42 [2]; **Stutsviken 2** [locus typicus restrictus], beach outcrop of reefal carbonates, ca. 10 m W of fishing huts [SW106: 28]; **Stutsviken 3**, patch reefs ca. 100 m W of Stutsviken 2, beach outcrop [SW107: 16]; **Balsklint**, crinoid shales (Höglint beds?), Br103389 [1].

Xanthea scabiosa n. sp.

Pl. 21A, figs. a–u; Pl. 21B, figs. a, b; Figs. 60, 61

Type locality and stratum. 'Snäckgärdet, Visby': this is the type locality from which the well-preserved holotype, and 35 paratypes are derived from the Upper Visby beds: no other precise collecting data is available, but it appears to represent a patch reef setting. It is not known if this is equivalent to the Snäckgärdsbaden 1 locality. An alternate locus typicus restrictus at which the species is common is Kneipbyn 3, coastal cliffs about 2 km SW of Visby: here are richly fossiliferous shales of the upper part of the Upper Visby Formation, Rövar Lilja Member, directly adjacent to and around small, 1–1.5 m thick coral patch reefs [61 Visby NO 89800–89900:45700–45800]. The type stratigraphic occurrence of this species lies within the *murchisoni* Zone (early Wenlock, lower Sheinwoodian), but it could range into the *riccartonensis* Zone (middle Sheinwoodian). The species occurs most commonly in nests and shaly pockets in and around small Upper Visby patch reefs, and is the most common atrypid at such sites, and the next most abundant brachiopod after rhynchonellids. Directly in and around Visby, Hedström (1910, p. 1474) stated that "the marl nests occurring in the reefs are frequently paying lodes for fossils". This certainly applies to the occurrence of this species in many of the smaller, Axelro-type reefs cited for the Upper Visby beds by Riding and Watts (1991). The species continues to be common in the Höglint patch reefs, but is apparently not as abundant there as in the lower levels. I have not seen it in reefs of the Kopparsvik (Tofta) Formation.

Diagnosis. Small, biconvex – weakly dorsibiconvex, wider than long, averaging 12 mm, 5–6 mm deep; relatively long hinge line; carination by divergent ventral mid-rib pair; sharply defined, narrow anterior fold.

Description. Small, biconvex to weakly dorsibiconvex; long, relatively straight hinge, indented hinge line, generally sharp

hinge corners in adult stages; wider than long; widths averaging 9–13 mm, depths averaging 5–6 mm; maximum width <26 mm, maximum depth <15 mm; generally somewhat flattened shell, twice as wide as deep; anterior commissure with high, narrow, U-shaped fold usually capped by 2 dorsal ribs; beak projecting; area prominent, sharply defined, orthocline; relatively large, apical or transapical foramen; distinct deltidial plates commonly wrinkled, thick; vv possessing divergent, raised mid-rib pair divided by 1 or 2 fine ribs in adult stages; dorsal valve with evenly sized ribs; ribs relatively coarse, 10–11 ribs in adult shell, spaced at ca. 3 per 5 mm, expanding in size distally; growth lamellae slightly projected, evenly spaced at 1.5–2.5 mm, crowded on commissure in adult shells, frills lacking. Interior of vv lacking pedicle callist; deltidial plates distally retracted into pedicle cavity; teeth solid, short, possessing small lateral lobes, distally with notch to accommodate crura; dv with strong socket plates, expanded, thick inner socket ridges dividing relatively wide central pit; very small crural bases and crura. Jugal processes and spiralia not sectioned.

Remarks. This species is distinguished from *Xanthea lamellosa* (Lindström, 1861) and *Xanthea haruspex* n. sp. in its much smaller size, stronger ventral carination, longer hinge, and wider than long shell.

Materials. Total 164 specimens. Upper Visby beds – Höglint Formation, early Wenlock. *Upper Visby beds*: **Snäckgärdet**, Visby sn., type locality, Br107475–494 [20], Br115491–4 [4], Br47384–7 [4], Br130711–8 [8]; **Snäckgärdsbaden 1**, Visby sn., Br108464–5 [2]; **Visby** (Lindström colln.), Br102557 [1], Br102560–70 [21], Br102572–4 [3]; **Kopparsvik**, Visby sn., Br122586–90 [5], Br113010–6 [7], Br131273–7 [5], Br131285–95 [11], Br47389 [1]; **Randklint**, Stenkyrka sn., Br11096 [1]; Klinten NV om **Kneipbyn**, Br108466 [1]; 'Visby B', Br11101–8 [8], Br41771–91 [21], Br47320 [1]; **Norderstrand**, Visby sn., Br41909 [1]; *Höglint beds*: **Rövar Liljas Håla**, Vasterhejde sn., Br134276–

Fig. 60. *Xanthea scabiosa* n. sp. Scatter diagrams and frequency curves pooled for all specimens from the Upper Visby beds and Höglint Formation, early Wenlock; camera lucida drawings of beak area in large adult shell.

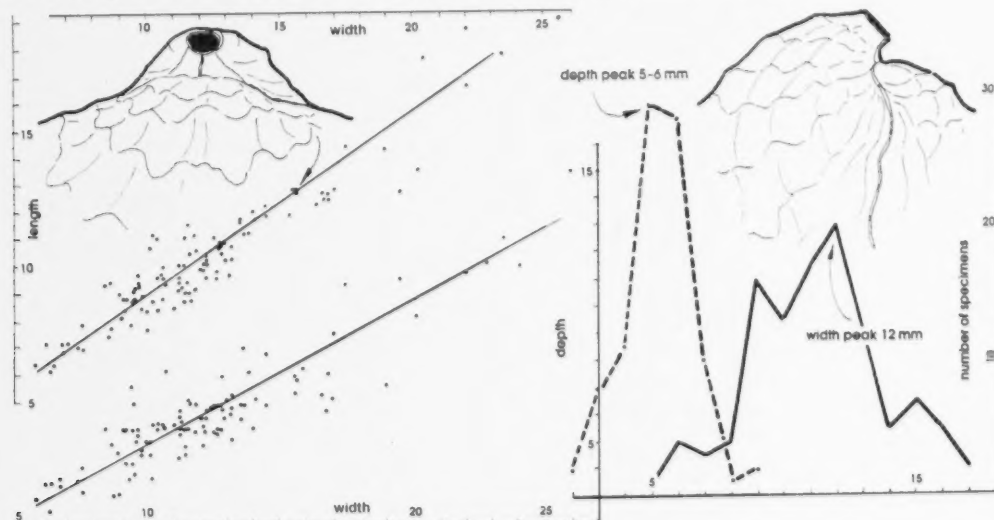
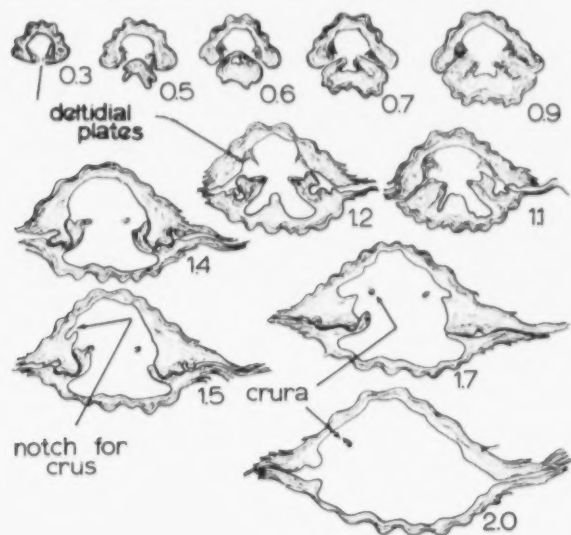


Fig. 61. *Xanthea scabiosa* n. sp. Serial sections of specimen Br103410, 'Korp-klint, Höglintskalk', early Wenlock, lacking spiralia and jugal processes: note inwardly retracted deltidial plates, very prominent inner socket ridges, $\times 5$.



77 [2], Br13440-3 [4]; **Galgbacken**, Visby sn., Br115552 [1]; **Lilla Klinten**, S om Korpklint, Br103435-7 [3]; **Korp-klint**, Vasterhejde sn., Br103393 [1], Br103395-416 [21], Br103424-5 [2]; **Kneippbyn 3**, coastal cliffs, ca. 50 m S of skjutfält barrier, Upper Visby beds with patch reefs [SW7: 4].

Xanthea haruspex n. sp.

Pl. 22A, figs. a-x

1928 *Atrypa imbricata lamellosa*, Munthe et al., p. 26-27 [for Solklint reef locality faunal list].

Type locality and stratum. **Fjaugen**, small island ca. 2 km NE of Kyllaj, 88900:08500, Othem sn., Slite beds, middle to upper parts, probably the reefal strata of unit 'G', called the Ryssnäs Limestone by Hede (1960, p. 70-71; see also Laufeld et al., 1978). This locality is rich in tabulate corals (heliolitids), stromatoporoids, crinoids, and bryozoans, suggesting that this is a patch reef or mudmound facies. The stratigraphic level of this species lies within the *ellesae* and *lundgreni* zones, i.e., middle Wenlock, but if British specimens from the higher parts of the Wenlock Shale and lower Dudley Quarried Limestone are included (as they tentatively are here), it extends the range of this species into the *nassa* and lower *ludensis* zones.

Diagnosis. Coarsely ribbed *Xanthea* with the ribs showing considerable size equalization, losing their carination, weaker anterior fold. Shells 15-20 mm wide or wider, as wide as long or slightly wider than long.

Description. Shell fairly well rounded in outline, biconvex - weakly dorsibiconvex, medium sized, ranging from about 15 to 20 mm in adult size, maximum 21.5 mm, slightly wider than long to equally wide/long, averaging 8-10 mm

deep, maximum about 12 mm, hinge line with weak indentation, hinge corners angled at 120° - 135° , beak protrusion blunt; orthocline to slightly apsacline area; foramen commonly expanded into ventral umbo, transapical, prominent, surrounded by distinct deltidial plates. Ribs initially somewhat fine in early stages, expanding rapidly towards anterior of shell, coarse, total only about 7-8 ribs on most adult shells, 10-11 ribs on largest shells; weak carination (with 1-3 ribs in ventral trough), or almost non-carinate, with equally sized ribs but rib enlargement along shell axis. Growth lamellae wave-like, upwardly deflected at breaking point, spaced at 1.5-2 mm, with no spines observed. Anterior commissure weakly arched, rarely U-shaped. No serial sections were made.

Remarks. This species differs from earlier forms in losing much of its carination, and in its *Eospinatrypa*-like appearance, with rounded shell, and less angular hinge corners. It is a rather scarce species confined to the middle Slite beds of the NE part of Gotland. Dudley is the only known location of the genus *Xanthea* in Britain, suggesting that it arrived there only in late Wenlock time. Some adult specimens of *Eospinatrypa asperula* (Davidson, 1882) from the Wenlock Limestone at Dudley may be difficult to separate from immature specimens of *Xanthea haruspex*, since the divergent enlarged mid-rib pairs on the vv are not always well developed until the shell reaches a larger size. *Eospinatrypa* can be distinguished by its lack of carination and enlargement of ribs on the vv. This species so closely approaches *Eospinatrypa*, the earliest of which occur in the overlying late Wenlock Halla Formation of Gotland, that it is highly probable that *X. haruspex* was the ancestor of, or link to, *Eospinatrypa*, e.g., *Eospinatrypa hallae* n. sp., an example of an atrypid missing link.

Materials. Total 16 Gotland specimens, from the reefal middle Slite beds, mostly around Othem parish. Type locality, **Fjaugen**, on small island ca. 2 km NE of Kyllaj, 889:085, Hellvi sn., Br105776, Br105878-81 [4]; **Slite Solklint**, N ändan, Slite, Othem sn., Br105873-7 [5], Br105871 [1]; **Lännaberget**, about 1 km N of Slite harbour (possibly the Lännabergets quarry figured in Munthe et al., 1928, p. 25), Othem sn., Br48104 [1]; **Slite**, Othem sn., Br107444 [1]; **Lotsbacken**, Othem sn., Br43930 [1]; **Barabacke**, Hörsne sn., Br43595 [1]; **Hydenk**, Hellvi sn., Br121780 [1]. Another locality appears to have been a reefal raukar, about 1 km SSW of Länna, and 1 km W of the centre of Slite (see Kartbladet Slite, in Munthe et al., 1928, p. 26). In Britain, 8 specimens came from collections labeled as 'Wenlock Limestone' around Dudley: these are derived from late Wenlockian strata, but comparable material from Gotland suggests that these specimens probably were from lower quarried limestone at Dudley, and possibly equivalent to the Farley Member of the Coalbrookdale Formation (the old 'Tickwood beds'); **Dudley**, 'Wenlock Limestone' [probably the Lower Quarried Limestone unit], BMB20701 [1], B610 [1], B23220 [1], B24029 [3], B5541 [1]; a shell, labeled as 'Dudley', is known from the Holcroft collection (#634; see Pl. 22A, figs. o-q), Birmingham University Lapworth Museum.

Subfamily Spinatrypinae Copper, 1978

Diagnosis. Coarsely ribbed, often large Atrypidae with wave-like growth lamellae; rib crests usually projected as short spines, capidulae, or short growth lamellae; small, generally reduced orthocline to anacline area; apical foramen surrounded by deltidial plates; relatively thin shell wall with delicate hinge structure; teeth with dental cavities; jugal processes tipped by short jugal plates; dorsal spiralia usually with many whorls.

Eospinatrypa Copper, 1973[= *Morinatrypa* Havlíček, 1990]

Type species. *Atrypa nodostrata* Hall 1857, Lockport, N.Y., Rochester Shale, Wenlock.

Diagnosis. Relatively small-medium, coarsely ribbed shells, with widely spaced growth lamellae periodically uplifted by wave-like growth of the thin shell; short, stubby spines or pseudo-spines (capidulae), possibly also short, rather smooth frills or no spines; small to large dental cavities, unfeathered crura; jugal processes strong, arched; conical spiralia filling much of shell.

Remarks. The genus usually has coarse ribs, with spines showing on well-preserved shells, and wavy, imbricating short growth lamellae, but it lacks the sharp fold and carination of *Plectatrypa* and *Xanthea*, as well as differing internally in having dental cavities, slender teeth, and socket plates, and no retraction of the deltidial plates inside the pedicle cavity. The surface micro-ornament of *Eospinatrypa asperula* (Davidson, 1882) is identical to that seen in the genus *Xanthea*, consisting of very fine, subconcentric zigzag filae. The shell interior lacks the thick shell wall and numerous overlapping growth lamellae of *Plectatrypa*, and the thick pedicle callist of *Atrypa*. Some of the more coarsely ribbed *Oglupes*, such as *O. davidsoni* (Alexander, 1947), somewhat resemble *Eospinatrypa*, but the clear resemblance of *Eospinatrypa asperula* to *Xanthea haruspex* suggests that the link to the *Spinatrypa* group lies via *Xanthea*, and not *Oglupes*. Some *Eospinatrypa* show that spines may develop only partially on the shell, or be capidulate, with the remainder of the shell showing short frills. This strongly suggests that the presence of both frills and spines on the shells indicates considerable early variability in this morphology, and that possibly not all Spinatrypinae possess spines. Some Givetian and Frasnian *Spinatrypa* from North America also appear to lack spines, as these are rarely preserved. Considerable caution must therefore be used in using spinosity as a primary feature for generic differentiation. The type species, *A. nodostrata* may have been poorly chosen (Copper, 1973), as it retains some of the nodular rib construction typical of *Plectatrypa*, and may not be typical of the genus; it needs to be re-examined because internal structure is unknown. The genus *Morinatrypa* (Havlíček, 1990) is of doubtful status, as it is based on very rare specimens whose internal structure is unknown, and appears indistinguishable from *Eospinatrypa*. It is evident that the earliest true spinatrypines appear in the late Wenlock.

The genus *Eospinatrypa* is generally a rare component of the Wenlock Gotland and British faunas, forming a trivial part of the brachiopod community, except in the Halla oolites where it is almost the only atrypid species, although never abundant. It seems to be absent in Ludlow strata on Gotland. Its distribution is primarily in the reefal, peri-reefal, oolitic, or biostromal facies, and its common and almost exclusive occurrence (to the absence of other atrypid taxa) in the Halla oncolitic to oolitic, and rare bryozoan patch reef facies, suggests that it was well adapted to a novel, current-moved sedimentary regime. In Britain *Eospinatrypa* seem confined to the reefal and peri-reefal Wenlock Limestone belt. It was not found in the deeper water Mulde facies equivalent to the southwest of Gotland. This is in contrast to Devonian occurrences, where *Spinatrypa* sees its richest development in deeper, or quieter water, lagoonal, back-reef muddy bottoms. The relationship of the Late Silurian-Devonian genus *Spinatrypa* Rzhonsnitskaya 1964, or to externally homeomorphic Devonian taxa such as *Invertina* Copper and Chen 1995, to such Silurian species of *Eospinatrypa* is also not clear at present.

Species assigned.

Atrypa asperula Davidson 1882, Dudley Limestone, middle-late Wenlock.

Terebratula cybele Barrande 1847, Prague Basin, upper Motol Fm., late Wenlock.

Atrypa nodostrata Hall 1857, Lockport, N.Y., Rochester Shale, Wenlock.

Reticulatrypa variabilis Johnson, Boucot, and Murphy 1976, Nevada, Wenlock.

Eospinatrypa sagana Boucot, Johnson, and Zhang, 1988, SE California, Hidden Valley Dolomite, Wenlock.

Eospinatrypa asperula (Davidson, 1882)

Pl. 22B, figs. c-l; Fig. 62

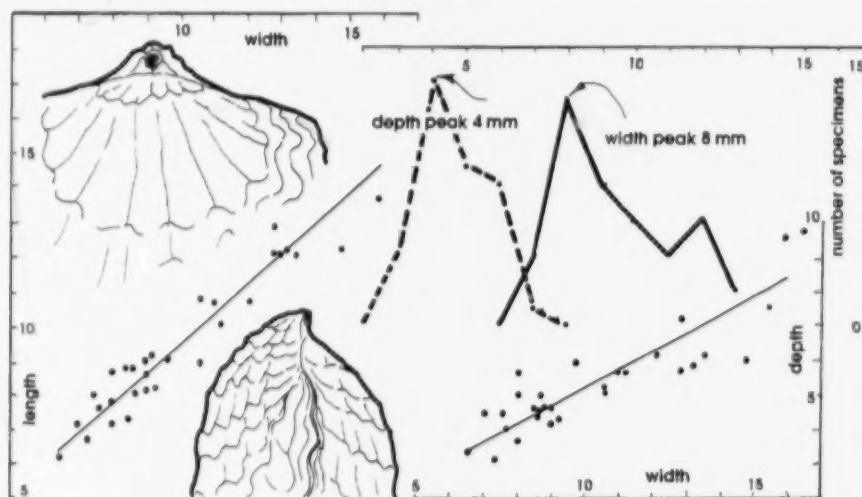
1867 *Atrypa reticularis* Linnaeus, Davidson, pl. 14, figs. 21-22.

1882 *Atrypa asperula* Davidson, p. 112-113, pl. 4, figs. 8, 8a.

1988 ?*Atrypa* ex. gr. *reticularis*, Antoshkina and Beznosova, pl. 1, figs. 6-8.

Type locality and stratum. In the original illustration the collecting locality is cited as 'Wenlock Limestone, Dudley' (Davidson, 1867, explanation to pl. 4), but Maw apparently later made larger collections at Benthall Edge, and Davidson (1882) thus also added 'Old Wenlock Limestone quarries at Benthall Edge'. The lectotype selected by Cocks (1978) is from the Much Wenlock Limestone of Benthall Edge, the second locality picked by Davidson (1882), when he described the species. Both localities indicate a late Wenlock age (Homerian, *nassa-ludensis* zones). The species also occurs in the Tickwood beds (*ludensis* Zone). Most abundant collections are from the West Midlands, at Dudley, but I was unable to find them in the same nodular limestones as the occurrence of *Endrea lonsdalei* or *Plectatrypa imbricata*. Their precise level may thus be in the limestones above or below the nodular beds. Maw's collections at Benthall Edge

Fig. 62. *Eospinatrypa asperula* (Davidson, 1882). Statistical variation in width, depth, length relationships based on compilation of all data, late Wenlock. Camera lucida drawing of average shell, approx. $\times 8$.



may have been derived from the Coalbrookdale equivalents, i.e., the Lower Quarried Limestone at Dudley, but only two specimens were available from there in the BMNH, contrary to data published. Most specimens came from the Sedgwick Museum and Geological Survey collections.

Diagnosis. Generally small, biconvex shells, averaging 8 mm wide, 4 mm deep; gently plicate to rectimarginate commissure; 7–9 expanding ribs on vv; slightly overlapping short growth lamellae, capidulae at some rib–lamella intersects.

Description. Small–medium shells, slightly wider than long, weakly biconvex, rounded to slightly shield-shaped; maximum gerontic width <20 mm, average 8 mm wide, twice as wide as deep, average 4–5 mm deep; small, pointed beak, apical foramen, orthocline area; ribs expanding distally, generally ca. 3 distally expanding ribs per 5 mm, total ribs on average specimen 8–9 on dv; growth lamellae short, spaced at 1–1.3 mm, producing short, curved aborted 'spines' at rib intersects; anterior commissure rectimarginate – weakly plicate. Internal structure unstudied.

Remarks. This species is distinguished from *Eospinatrypa hallae* n. sp. by being about half as wide, generally wider than long, and only weakly biconvex, possessing a rectimarginate commissure. *E. asperula* is smaller than *E. cybele* (Barrande, 1847) and has fewer ribs and a nearly rectimarginate commissure. Young specimens of *E. hallae* are somewhat similar to the Davidson species, and may be difficult to distinguish except by the coarser ribs. A statistical comparison, based on a relatively small collection of both species, totaling fewer than 60 specimens, is probably not adequate to tell these species apart. In SEM detail of the shell surface, *E. asperula* has a zigzag micro-ornament similar to that of *Xanthea* (Fig. 97), confirming the relationship of the genera. No spines were found on any specimens. No specimens were found in Gotland collections.

Materials. 52 specimens. 'Dudley, Wenlock Limestone', A26613 [1], A26636 [1], A26639–42 [4], A26644–57 [14],

A26795–8 [4], BB55300–2 [3], GSM12301 [1], GSM103757–63 [7], GSM61162–4 [3], GSM103745–56 [12]; Tickwood, Tickwood beds, B1583 [1]; Benthall Edge, 'old limestone quarries', ?Coalbrookdale Fm. BB66829 [1].

Eospinatrypa hallae n. sp.

Pl. 23A, figs. a–o; Figs. 63–65

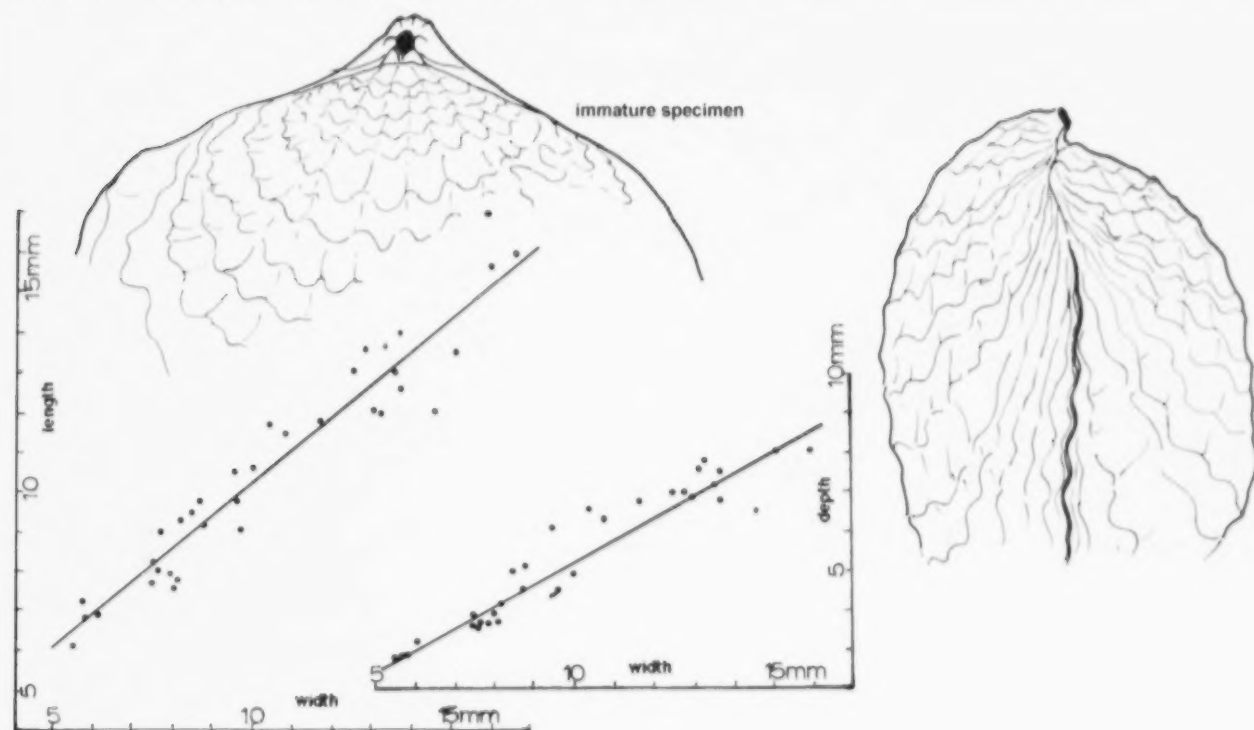
1828 *Atrypa aspera* Schlotheim, Dalman, p. 128–129, pl. 4, figs. 3a–c.

1837 *Atrypa aspera* Schlotheim, Hisinger, p. 75, pl. 21, figs. 12a–b [copy of Dalman figures].

?2001 *Eospinatrypa* sp., Rong and Zhang, p. 93–94, pl. 52, figs. 1–8.

Type locality and stratum. *Hörsne kanalen 1*, 'Hörsne, kanalen V om bron, övre revkalk', Hörsne canal west of the spring. This locality is apparently no longer exposed, and its precise location is unclear from the Riksmuseet collection: I was unable to collect fresh material, although the oolite is exposed in the area (Laufeld, 1974). The presence of such specimens must have been known to Hisinger (1828), and Dalman (1828), who was the earliest to illustrate material that fits the description of this species. The collecting level is the 'upper reef' limestone of the Halla Formation, which is generally a thickly bedded oolite, with local, small bryozoan patch reefs. The Halla Formation is said to be the partial time equivalent of the Mulde Marl to the west, thus lying mostly within the *nassa* Zone, of mid-Homerian, late Wenlock (pre-Klinteberg) age, according to Bassett, Kaljo, and Teller (1989). Laufeld and Jeppsson (1976) placed the Halla Formation within the upper *lundgreni* through *nassa* zones, which seems more appropriate. The inferred paleo-environment is a high-energy, wave and storm-disturbed, shallow carbonate, Bahama-type, sandy-oolid, shoal habitat. *Eospinatrypa* is absent in the deeper water Mulde Marl of Gotland.

Fig. 63. *Eospinatrypa hallae* n. sp. Statistical comparison of width, length, depth compiled from all specimens in the Halla Formation, middle Wenlock. Camera lucida drawing of mature shell.



Diagnosis. Relatively large sized, elongate *Eospinatrypa*; average 13–16 mm wide; slightly enlarged, bifurcating mid-rib pair on the vv; 12–15 ribs on larger shells; small erect, orthocline beak; small deltidial plates. Internally, with long jugal processes, terminally spinose, with small jugal plates; up to 9 spiral whorls.

Description. Shell well rounded to elongate, globose in adult stages, usually longer than wide, adult shells average 13–16 mm wide, maximum width <20 mm, normally <8 mm deep; beak minute, somewhat pointed; orthocline area with small apical foramen, minute deltidial plates (holotype, a large shell, shows anacline area incurvature, transapical foramen). Hinge line weakly indented; angular to rounded hinge corners; apical angle 110° – 115° ; anterior commissure weakly folded, in adult shells with relatively narrow, low dorsal fold; ribs relatively fine in first 5 mm of shell growth, then coarsening rapidly, with slightly stronger mid-rib pair bifurcating on the ventral crest, 3–4 ribs on each side, 2–3 ribs per 5 mm; spines short, stubby, irregular, preserved best on ventroposterior side, with nodes clearly visible on decorated shell, demarking probable former spine bases; concentric growth interruptions, or short overlapping growth lamellae, about 1 mm apart, consistent during growth, packed along commissure in gerontic shells. Internally, thin shell, weakly impressed, or unimpressed muscle scars; pedicle cavity vacant, lacking pedicle callist; delthyrium displaying minute, short deltidial plates; teeth short, blunt, lacking distinct lateral lobes; dental cavities small, rounded; hinge plates thin, delicate; socket plates with strong inner socket ridges; crura

arched, non-feathered; long, jugal processes thick, prominent, terminating in nodose ends; delicate, sharply medially bent jugal plates; spiralia filling most of shell cavity, <9 whorls.

Remarks. The average shell is about 50–80% larger, and more elongate, globose, than *E. asperula* (Davidson, 1882), but small specimens are similar in many features except that *asperula* is more coarsely ribbed in early ontogenetic stages. The species is quite similar to *E. cybele* (Barrande, 1847), as illustrated by Havlíček (1990), at about 50% larger, has twice the number of ribs, and lacks a strong anterior fold. In terms of size and shape, the species is almost perfectly illustrated in Dalman (1828), who referred it to the widely known Devonian species from the Eifel, *Spinatrypa aspera* (Schlotheim, 1813). Dalman stated it came from the Hisinger collection, and cited 16 ribs for the shell, the same figure within the range seen in the Halla material. Dalman's figures were later copied by Hisinger (1837). Curiously, no *Eospinatrypa* occur higher or lower in the sequence in Gotland, despite the presence of suitable shallow high-energy facies such as the Eke-Burgsvik strata. No similar specimens are known from Britain, where they should occur in the upper Much Wenlock Limestone.

Materials. Total 35 specimens Halla Formation: mid-Homerian, late Wenlock. **Hörsne kanalen 1**, 'V om bron, övre revkalk', Br105910–11 [2], Br105918–22 [5], Br105923–28 [6]; **Hörsne kanalen 2**, 'O-andan, cephalopodenkalk', Br105912 [1]; **Hörsne kyrkan**, 'kanal vid kyrkan', Br105913–17 [5]; **Gandarve kvarn**, Dalhem sn., Br107447–64 [15].

Fig. 64. *Eospinatrypa hallae* n. sp. Serial sections of mature shell, Br105917, from type locality, Hørsne kanalen, Halla Formation, middle Wenlock; note large expansion of spiralia in dorsal cavity, $\times 5$.

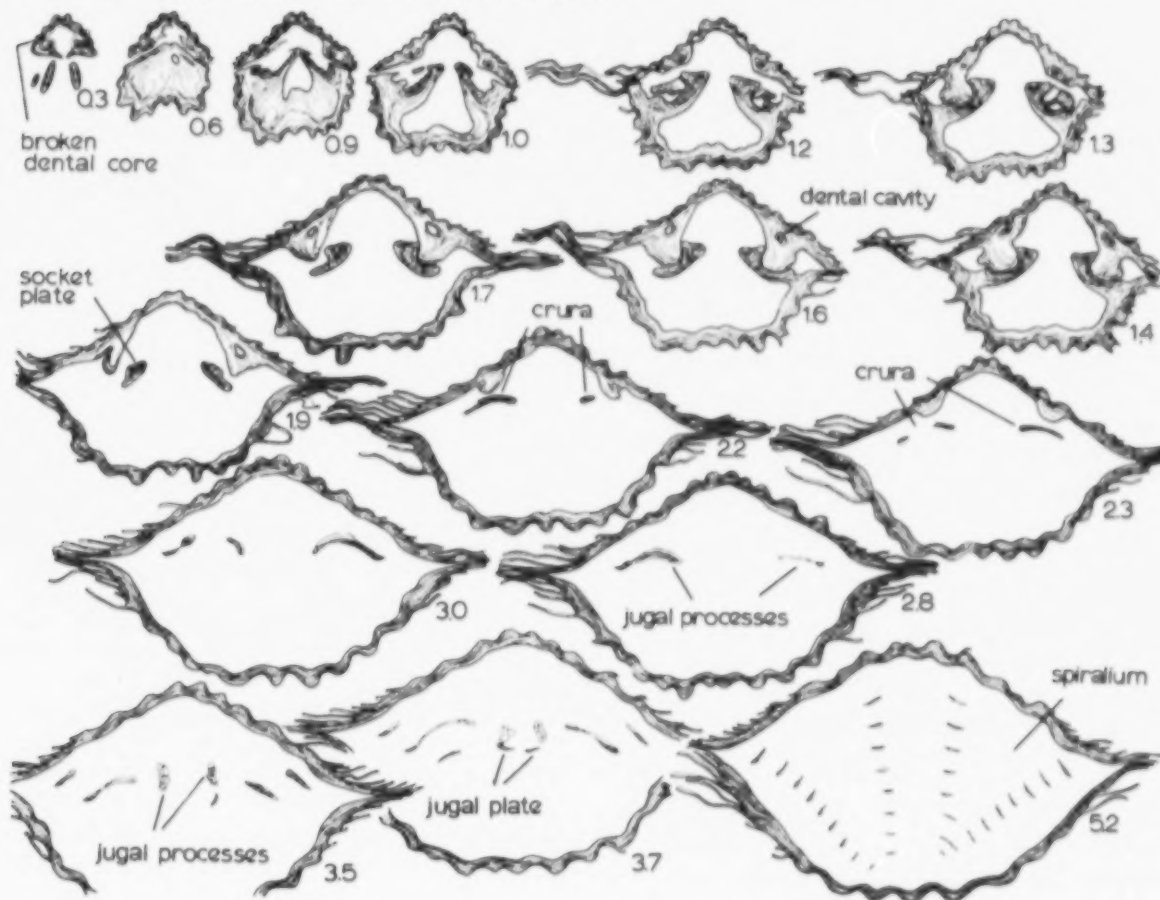
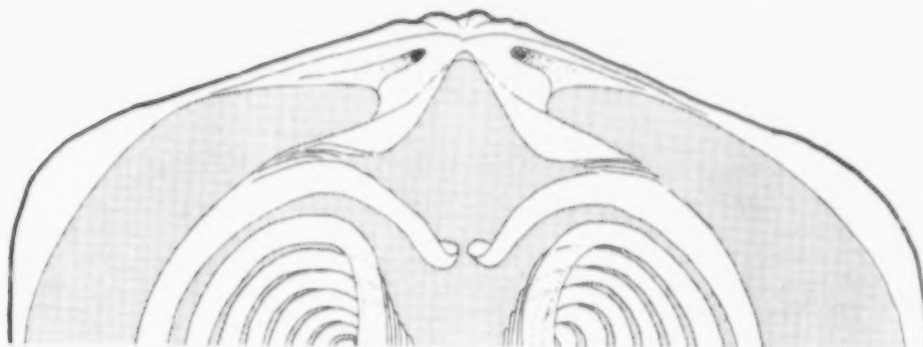


Fig. 65. *Eospinatrypa hallae* n. sp. Reconstruction made from serial sections of Br105917, Hørsne kanalen, Halla Formation, middle Wenlock; $\times 10$.



Subfamily Spirigerinae Rzhonsnitskaya, 1974

[= Schachriomoniinae Rukavishnikova, 1982; = Pectenospirinae Popov, Nikitin, and Sokiran, 1999]

Diagnosis. Biconvex to dorsibiconvex, relatively small to medium sized, carinate; prominent, apsacline-anacline area; distinct delthyrium with deltidial plates, apical foramen; sharp anterior fold defined by prominent diverging ventral mid-rib pair on dv; continuous, tubular ribs featuring concentric filae; growth lamellae rare, frills absent, skirt sometimes present; pedicle callist normally absent; teeth with dental nuclei, or elongated, slit-like dental cavities; jugal processes disconnected, curved centrally, tipped by small, laterally directed jugal plates; spiralia dorsally directed.

Genera assigned. *Spirigerina* Orbigny 1847; *Eospirigerina* Boucot and Johnson 1967 (= *Zanclorhynchula* Xu 1979a; = *Eorhynchula* Liang 1983a; = *Neorhynchula* Liang 1983b), *Ogilviella* Lenz 1968 [= *Arctospira* Smith 1980]; *Neospirigerina* Rzhonsnitskaya 1975; *Schachriomonia* Nikiforova 1978; *Sulcatospira* Xu 1979c [= *Antizygospira* Fu 1982; = *Ovalospira* Fu 1982; = *Tauquospira* Fu 1982; = *Kazgunia* Misius, in Klenina 1984, vide Misius, 1986]; *Qilianotryma* Xu 1979b [= *Euroatrypa* Oradovskaya 1982, see also Oradovskaya 1983; = *Orthocarina* Fu 1982]; *Qiarella* Rukavishnikova 1982 [nomen nudum]; *Australispira* Percival 1991.

Range. Caradocian-Emsian.

Spirigerina Orbigny, 1847

Type species. *Terebrantula marginalis* Dalman 1828, Klinteberg, Gotland, late Wenlock [by subsequent designation, Alekseeva, 1960b, following d'Orbigny, 1850; Lindström, 1861].

Range and distribution. Aeronian-Emsian; worldwide, except Malvinokaffric realm.

Diagnosis. Shells medium sized, biconvex dorsibiconvex, commonly with pointed, protruding beak; apsacline-orthocone area; prominent apical foramen, deltidial plates; fine to moderately sized, continuous tubular ribs; short, overlapping growth lamellae at commissure; frills not known, skirt rare; distinctive fine radial and concentric filose micro-ornament; dorsal fold rounded, broad to sharp. Internally, prominent hollow, thick deltidial plates; pedicle callist thin or absent; teeth short, blunt, flat-sided, with small lateral processes; dental nuclei slit-like, usually expanding to large dental cavities and 'dental plates', accommodating distal notch for crura; moderate to thick hinge plate; thin socket plates with massive inner socket ridges; small crural bases, delicate, simple, non-fibrous crura; jugal processes simple, straight, curved in shell centre, terminating in thin, flat jugal plates directed laterally; spiralia dorsally directed, normally <8 relatively thick, widely spaced whorls.

Remarks. Schuchert and Cooper (1930, p. 278) used the name *Plectatrypa* (type, *Atrypa imbricata* Sowerby 1839) for the 'marginalis' portion of 'Atrypa', which they stated was known for 'forming a long and distinct line' [indeed in the literature, since 1828, 'marginalis'-type atrypids were traditionally separated from all others]. However, Alekseeva (1960b) was first to perceive that the *marginalis* lineage was quite different from the *imbricata* lineage that Schuchert and Cooper had in mind, in possessing continuous ribs lacking

imbricate growth lamellae. She thereby resurrected and clarified d'Orbigny's (1847) genus *Spirigerina*, which had remained generally dormant in the literature for about a century (except for use by Lindström in Gotland). D'Orbigny (1847) himself had never properly defined his genus, although he must have had access to specimens from Gotland, widely distributed in museums in the 19th century. Alekseeva (1960b) thus separated d'Orbigny's *Spirigerina* from *Plectatrypa*, with which it had commonly been confused. In 1974 Rzhonsnitskaya appropriately raised the spirigerines to subfamily status. Boucot and Johnson (1967) further separated from the genus *Spirigerina* those species of Ashgill through early Llandovery age, naming the ancestral species-group *Eospirigerina*. *Spirigerina* is externally distinguished from *Eospirigerina* by its development of tubular ribs, and sharply defined microgrowth lines (i.e., filae), a larger and more protruding beak, marked deltidial plates, and distinct anterior fold defined by a very prominent mid-rib pair on the vv (see also Boucot and Johnson, 1967). Internally, *Spirigerina* possesses a very thick hinge plate, teeth with slit-like dental cavities, and minute crura. However, the two genera grade into each other, and are not always easy to distinguish, except internally, and there is yet no published data on the internal structure of *Eospirigerina*. This awaits publication of the revision of Anticosti Atrypida.

Spirigerina is larger and much more coarsely ribbed than the Late Ordovician (Caradoc-Ashgill) genus *Sulcatospira* (Xu, 1979c), which appears to be a finely ribbed ancestor of *Eospirigerina*. Oradovskaya (1982) assigned the finely ribbed Siberian spirigerine *Euroatrypa* (= *Qilianotryma*) to the Clintonellinae, the genus probably derived from the finely ribbed spirigerines via loss of carination and loss of commissural fold. In that sense *Qilianotryma* shares similarities with the very finely ribbed Chinese Silurian genus *Beitaita* (Rong, Xu, and Yang, 1974), which has the shape of the smooth genus *Septatrypa*, but the ribs of clintonellines. Poulsen (1943) used the name *Nalivkinia* (Bublichenko, 1927), another clintonelline, for members of the *marginalis* lineage, although clintonellines were undoubtedly derived from spirigerines. Rzhonsnitskaya (1964) defined *Neospirigerina* as late derived *Spirigerina* that had evolved a very coarsely ribbed, somewhat flat shell lacking a distinct fold and carination. Coarse ribbing began with *Spirigerina costata* from the Hemse beds (Lower Ludlow) and is very marked in *S. quinquecostata* from the Hamra beds (upper Ludlow), neither of which are assigned here to *Neospirigerina* because the Gotland species have an internal structure like *Spirigerina*. Clear definition of *Neospirigerina* awaits redescription of the Russian type species. Breivel and Breivel (1977) illustrated the internal structure of some Early Devonian *Neospirigerina* that suggests these have expanded, large dental cavities, a possible distinguishing character from Silurian species. It should be noted that there is a general trend towards dental cavity enlargement and more delicate teeth during Wenlock-Ludlow time in *Spirigerina*, with the last Gotland species *S. quinquecostata* having the largest dental cavities.

Lindström (1861) first used the name *Spirigerina* for the distinctive rhynchonelliform species from Gotland [following d'Orbigny, 1847], and distinguished two species, *S. marginalis* and *S. imbricata*. On the shell of *Spirigerina*, ribs on the ventral valve are most commonly intercalated and on the dorsal valve bifurcated, although this is not invariable. This method of rib multiplication is generally the opposite of that seen in most Atrypinae, e.g., for *Atrypa* and *Desquamatia*, where ribs on the dv are usually intercalated. The most noticeable feature in *Spirigerina* from Gotland and Britain is the evolutionary trend towards rib coarsening during the Wenlock–Ludlow interval, from finely ribbed *marginalis* in mid- to late Wenlock time, to coarsely ribbed *quincocostata* in the late Ludlow. This trend is paralleled elsewhere and appears to provide a useful stratigraphic tool for the Wenlock. The oldest *Spirigerina* appear to be very small species of Aeronian (middle Llandovery) age, while *Eospirigerina* survived the end Ordovician mass extinctions into the Rhuddanian, although all the early species are poorly described.

Spirigerina appear to be typically associated with very shallow water, shoaling, peri-reefal, and reef environments in the late Wenlock and Ludlow of Gotland, being found with abundant corals and calcareous algae. They are locally common from reefal Klinteberg, Hemse, and Hamra facies, but usually occur in nests or clusters, possibly sheltered in reef cavities between large frame-builders, and may thus be easily missed. In this region, *Spirigerina* does not make an entry until the late Wenlock *nassa* Zone, probably a migrant from elsewhere, as the reef and biostrome niche on Gotland was initially occupied in the early and mid-Wenlock by *Xanthea*, *Plectatrypa*, and *Eospinatrypa*. On Gotland and Anticosti *Spirigerina* is absent in the deeper water facies, e.g., of the Slite beds, the Mulde Marl, and the SW facies of the Hemse beds. In contrast, Hurst (1975b) remarked that his '*Spirigerina*' was confined to the offshore, deep Wenlock *Eoplectodonta duvalii* community in Britain, and that *Spirigerina* was absent in the diverse shallow *Sphaerirhynchia* community. Hurst (ibid., p. 243) expressed doubts concerning the depths of the *Eoplectodonta* facies, and appears to have mistaken *Plectatrypa* for *Spirigerina*, much as did Sowerby, Davidson, and others. *Plectatrypa* occurs in deeper water and as well as peri-reefal facies. In Britain, I only found *Spirigerina* in pockets or nests associated with reef and off-reef calcarenites: in the Wenlock it is absent in the shaly distal reef and deeper water facies where *Atrypa* and *Plectatrypa* normally occur. *Spirigerina* is common in late Llandovery rocks of the Zeravshan region in Uzbekistan, in the Altai and China, which suggests that larvae probably migrated westwards, captured by tropical easterly currents from such areas [see below].

Species assigned. Some 40 species are now assigned to *Spirigerina*, excluding those referred previously to *Eospirigerina*. Some may refer to *Neospirigerina*. Most need revision:

?*Atrypa altijugata* Lindström 1880, Dalecarlia, Sweden, ?Wenlock.

Plectatrypa australis Philip 1962, Tyers, Victoria, Australia, Boola beds (?early Pragian).

?*Eatonina bicostata* Stauffer 1930, Nevada, ?Early Devonian [possibly *Neospirigerina*].

Spirigerina barkolensis Zhang 1981, Balikuan, Xinjiang, Wenlock.

Plectatrypa brownsportensis Amsden 1949, Tennessee, Brownsport Fm., Ludlow.

Atrypa calvini Nettelroth 1889, Kentucky, U.S.A., Wenlock.

Atrypa marginalis var. *costata* Lindström 1861, Gotland, middle-upper Hemse beds, early Ludlow.

Spirigerina convexiplata Su 1976, Bateobao, Inner Mongolia, Xibiehe Fm., Ludlow.

Spirigerina cuboidea Menakova 1964, Daurich, Zeravshan–Gissar Mtns., Bed 'N', Telychian, Llandovery.

Spirigerina dauritschensis Menakova 1964, Daurich, Zeravshan–Gissar Mtns., Bed 'G', Aeronian, Llandovery.

Carinata diana Kulkov 1974, Rossnaya, NW Altai, Yavorski beds, Telychian, Llandovery.

Spirigerina druida Havlíček 1987, Cerovy Schody, Prague Basin, Vinarice Lst., Pragian.

Spirigerina dubia Menakova 1964, Daurich, Zeravshan–Gissar Mtns., Bed G, Aeronian, Llandovery.

Spirigerina eximia Gratsianova 1967, Kamysensk, Altai Mountains, Remnev beds, Lochkovian (assigned to *Neospirigerina* by Mizens and Sapelnikov, 1982).

Atrypa expansa Lindström 1880, Fjeka Dalecarlia, Sweden, ?Wenlock.

Spirigerina grata Kulkov 1974, Kamysenskogo, N Altai, Chinettin Horizon, Yavorski beds, Telychian, Llandovery.

Nalivkinia groenlandica Poulsen 1943, 'the coast, lat. 80 degrees north', Greenland, Wenlock.

Spirigerina guangyinqiaoensis Wan 1982, Guanying Bridge, Qijiang, Sichuan, lower Hanjiadan Fm., Wenlock.

Spirigerina hoboksarensis Zhang 1981, Shabareti Mtn., Hoboksar, Xinjiang, Shabareti Fm., Wenlock.

Spirigerina hongduensis Rong and Yang 1981, Guizhou, Xiangshuyuan Fm., Aeronian, Llandovery.

Spirigerina intermedia Perry 1984, Yukon, Canada, '527–536 m below top Delorme Fm.', Lochkovian.

Spirigerina kuqaensis Zhang 1981, East Haliketao Mtn., Xinjiang, Keketiedaban Fm., Wenlock.

?*Spirigerina marginaliformis* Alekseeva 1960b, Urals, Petropavlovsk Fm., Lochkovian–Pragian.

Terebratula marginalis Dalman 1828, Klinteberg, Gotland, Klinteberg beds, late Wenlock.

Atrypa marginalis quincocostata Munthe 1911, Hoburg, Gotland, Hamra beds, late Ludlow.

?*Atrypa marginaloides* Nalivkin 1926, in Alekseeva 1962, Urals, Ems. [assigned to *Spirigerina* by Alekseeva].

?*Atrypa marginaloides* Nalivkin 1926, in Rzhonsnitskaya 1975, Altai Mountains, Yakushin beds, late Lochkovian–Pragian. [species attributed in literature to Nalivkin, 1926, p. 54; assigned to *Neospirigerina* Rzhonsnitskaya, 1975].

Trematospira mathewsoni McClesney 1868, Kentucky, Wenlock.

Spirigerina minor Kulkov 1967a, Ini River Basin, NW Altai, Chagyrskaya Suite, Wenlock.

?*Atrypa marginalis* var. *multistriata* Foerste 1890, Indiana, Clinton Group, Aeronian, Llandovery.

?*Plectatrypa ossa* Nalivkin 1960, Pai-Khoi, NE USSR, ?Ems.

- Atrypa pseudomarginalis* Hall 1867, New York, Rochester Shale, Wenlock.
- ?*Rhynchonella psittacus* Haupt 1878, glacial erratics, northern Germany, ?Ludlow-Pridoli.
- ?*Atrypa quasi-comata* Khalfin 1948, Gorno Altai, Early Devonian, ?Lochkovian.
- Plectatrypa marginalis sibirica* Rzhonsnitskaya 1960, Gurevsk, Malobachat Horizon, Pragian.
- Spirigerina sigismunda* Havlíček 1991, Prague Basin, upper Kopanina Fm., late Ludlow.
- ?*Spirigerina simplex* Su 1976, Bateobao, Inner Mongolia, Xibiehe Fm., Ludlow.
- Oxoplecia sinensis* Wang 1962, Guizhou, South China, ?late Llandovery [see Rong and Yang, 1981].
- Spirigerina subquadrata* Su 1976, Bateobao, Inner Mongolia, Ludlow [see Su et al., 1983].
- Plectatrypa sulevi* Jaanusson in Alikhova 1954, western Siberia, Llandovery.
- Atrypa supramarginalis* Khalfin 1948, Gorno Altai, Solovien Lst., Yakushinsk beds, Lochkovian.
- Plectatrypa transversa* Zhang 1981, Talir, Xinjiang, Kaoke-saikai Fm., Ludlow-Pridoli.
- Spirigerina uniplicata* Zhang 1981, Aoshike, Qinghe County, Xinjiang, Wenlock.
- Not assignable to *Spirigerina*:
- Spirigerina dulkumensis* Yadrenkina 1978, Bolshaya Nirudna R., Siberia, lower Dolbors Horizon, Caradoc (= *Sulcatospira*).
- Zygospira kueichowensis* Wang 1956a, Yingwuhsi, Guizhou, Lojoping Fm., Aeronian-Telychian, Llandovery [= ?*Clintonella*].
- Spirigerina* (*Neospirigerina*) *ossa transversa* Rzhonsnitskaya 1975, Malobachat R., Kuznetsk Basin, Pragian.

Spirigerina marginalis (Dalman, 1828)

Pl. 23B, figs. a-z, za; Figs. 66, 67

- 1828 *Terebratulina marginalis* Dalman, p. 143-144, pl. 6, figs. 6a-e [see Fig. 66].
- 1837 *Terebratulina marginalis*, Hisinger, p. 81, pl. 23, figs. 8a-c.
- 1880 *Atrypa marginalis*, Lindström, p. 22, pl. 12, figs. 11-16 [Klinteberg Fm., Lilla Karlsö].
- 1943 *Nalvikinia marginalis*, Poulsen, figs. 18a-d, 1; figs. 20h-k [from Klinteberg].
- 1967 *Spirigerina marginalis*, Boucot and Johnson, pl. 3, figs. 1-10.
- 2002b *Spirigerina marginalis*, Copper, fig. 970-2.

Type locality. 'Gotlandia, in Klinteberg' (Dalman, 1828), probably from the lower Klinteberg Formation, late Wenlock, Homerian, upper *nassa* (*deubeli*) or lower *ludensis* zones. The lower Klinteberg Fm. is partly equivalent to the upper Mulde beds (and therefore of upper *nassa* or *deubeli* zones). It is also likely that the strata exposed around Snoder, in 'Hemse facies', are of high Klinteberg age (*ludensis* Zone). The herewith designated type locality, **Klinteberget 1** (Laufeld, 1974), is the northwest side of an inland cliff in the town of Klinte, CJ 4625 6430. The locality today is mostly covered by vegetation and rubble from quarrying, and the exact horizon from which the abundant old collec-

tions were made is not certain, but the section intersects the lower and middle part of the Klinteberg beds. *S. marginalis* probably came from the lower part of the Klinteberg succession at Klinteberg (i.e., the *deubeli* Zone equivalents): loose specimens are rare. Judging from other localities, the species seems to occur in nest-like concentrations within or adjacent to reefs. Shells usually contain sparry calcite or a light yellowish to greenish micrite, and this suggests that the species was present in soft muddy pockets within the reef complex. The species was also discovered by Lindström (1880) on Lilla Karlsö Island. New collections made by Bassett and Cherns in 1990 from Lilla Karlsö show that *marginalis* is common at locality Bassett 90-55, within 200 m of the boat landing on the southeast coast: the precise level here within the Klinteberg Formation is not certain but probably also in lower levels, not much above the contact with the Mulde Marl. Bassett and Cocks (1974) deferred selection of a lectotype from the 45 specimens collected by Hisinger, and the lectotype selected herewith is Br105813, from the Hisinger collection (used by Dalman), matching most closely the Dalman figured specimen.

Diagnosis. *Spirigerina* with slightly wider than long, dorsibiconvex shell; 25-35 fine ribs of nearly equal size covering shell surface, maintaining size by frequent intercalation (dv) and bifurcation (vv); growth interruptions or very short growth lamellae frequent at adult commissure; beak prominent, protruding, orthocline to weakly apsacline; apical foramen, well-developed deltidial plates; apical angle 125°-130°; dorsal fold covered by 3-5 ribs, prominent, laterally divergent, U-shaped to squared, with distinct, distal small commissural lip or flange.

Description. Medium sized, average width 13 mm, maximum width 18 mm, slightly wider than long, lengths 12-15 mm, depths 6-9 mm; dorsibiconvex to dorsally globose in gerontic stages; ventral valve slightly convex to flat, only weakly carinate posteriorly; protruding to wide beak; apsacline to nearly orthocline area; apical angle 120°-130° to less than 110° in neanic stages; hinge line indented, concave; ribs more or less equally sized over shell surface; ventral mid-rib bifurcates early, forming double mid-rib pair, flanking fold in late stages; dorsal mid-rib normally bifurcating twice at fold crest; from apex, two divergent, lateral dorsal ribs enlarge distally; ribs tending to curve laterally, intersected by fine filae; in gerontic specimens overlapping growth lamellae at commissure; 9-15 ribs on shell flanks; 4-7 ribs on the fold-sulcus; up to 38 ribs on large adults; dorsal fold U-shaped, rounded, to slightly squared, prominent, relatively wide, commonly with small, but distinct lip. Internally, pedicle callist thin to absent; deltidial plates distinct, expanding only marginally into pedicle cavity, terminating in thin projections; teeth thick, wide; dental plates short, lining pedicle cavity and abutting slit-like dental nucleus; hinge plates massive; socket plates curved but thin; very large, bulbous inner socket ridges; cardinal pit narrow and grooved, with prominent, bifurcating median septum; crural bases small, rounded leading to thin, relatively straight crura; complete jugal processes and spiralia rarely observed, but spiralia with normally fewer than 6 whorls, jugal processes long, curved centrally and ending in laterally directed flat jugal plates.

Fig. 66. *Spirigerina marginalis* (Dalman, 1828). Statistical comparison of all specimens from type locality, Klinteberg 1, late Wenlock; selected camera lucida drawings of growth stages: upper row of line drawings from Dalman (1828), enlarged to scale of $\times 2$, matching lectotype Br105813.

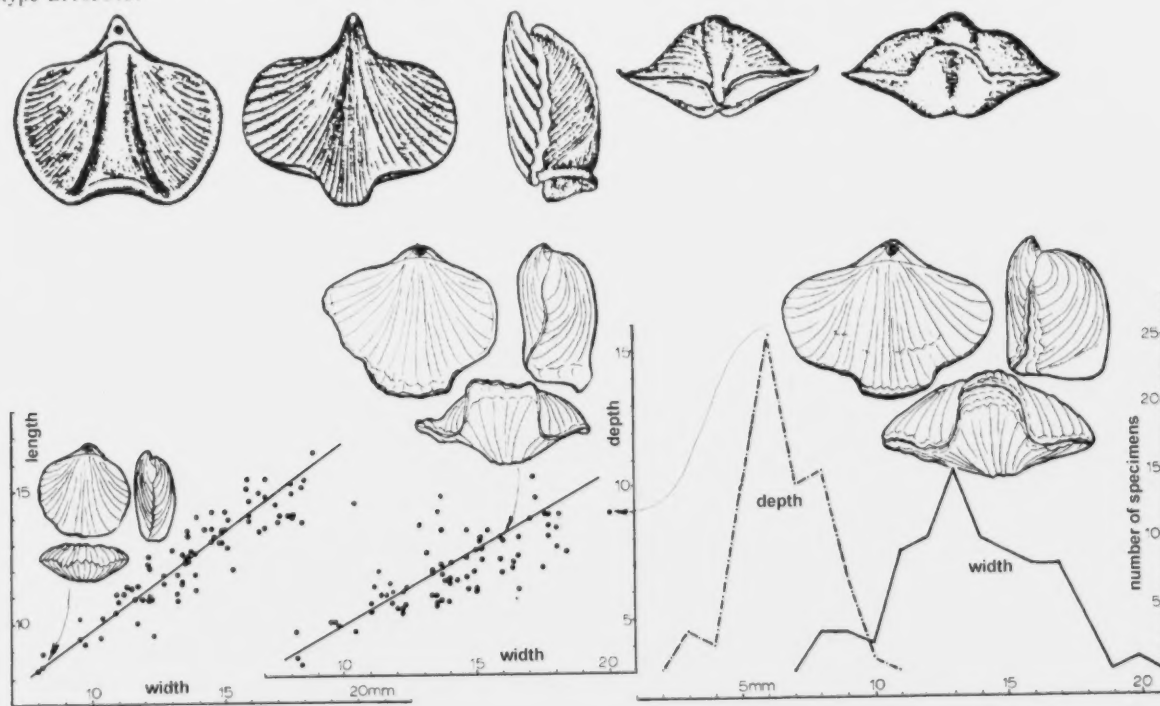
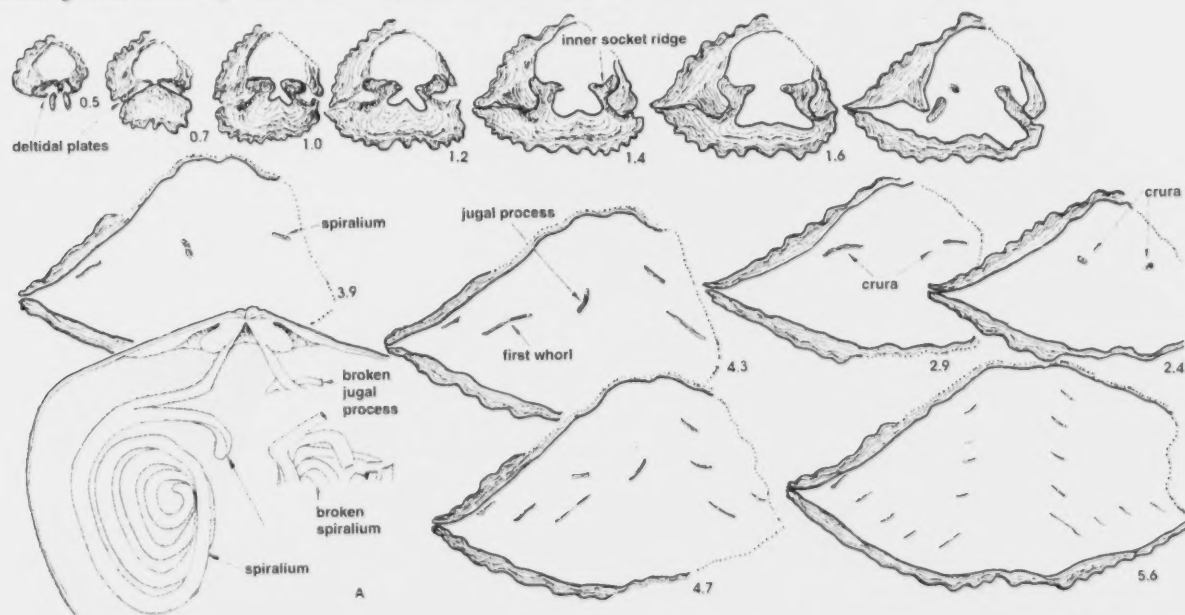


Fig. 67. *Spirigerina marginalis* (Dalman, 1828). Serial sections of two specimens. (A) Hypotype GS9051G, 'Klinteberg beds, Lilla Karlsö', late Wenlock; partially complete left spirialium, broken right spirialium, partly damaged shell (reconstruction of left spirialium and jugal process on lower left side, and incomplete, broken spirialium on right side); (B) serials, paratype Br41937, Hisinger colln., 'Klinteberg beds, Klinteberg', late Wenlock; specimen with partially preserved spiralia; $\times 5$.



Remarks. *Spirigerina marginalis* is a relatively finely ribbed species and therefore easy to distinguish from others in the West European Wenlock sequence. It is more finely ribbed

and smaller than *S. lockwenia*, which has up to about 20 ribs on the shell, instead of up to 38 ribs as in *S. marginalis*. The latter also has a more distinct, elevated, enlarged ventral

mid-rib pair, two troughs flanking the dorsal mid-rib, and usually an upturned dorsal flange. *S. marginalis* from the Klinteberg Fm. (very likely the high *nassa* to lower *ludensis* zones) appears to pre-date the arrival of *S. lockwenia* from the upper part of the Wenlock Limestone of Britain. The sequence of progressive rib coarsening stratigraphically upwards, as seen in Gotland, marks a distinct trend. *S. lockwenia* has not been found in the upper Klinteberg, nor lower Hemse beds, and is known only from Britain. Conversely, *S. marginalis* appears to be absent in equivalent British strata. Serial sectioning of several specimens, and examination of many others through light transparency, reveals that very few (<1–5%) of specimens have spiralia oriented in life position: nearly invariably the spiralia are broken and disoriented within the shell cavity. Very few specimens have a micritic infilling, most being infilled with calcite spar. This has made reconstructions of whole spiralia and jugal processes difficult.

Materials. Total 157 specimens from the Klinteberg Fm. 'Klinteberg', type locality = **Klinteberget 1** (Laufeld, 1974). The Wegelin and Hisinger collections were examined by Dalman (1828), and make up the following catalogued numbers, Br105809–838 [Hisinger colln. -30], Br42051–69 [15], Br123210–225 [16]; 'Gannarveskar, Frojel sn.', Br41618–22 [5]; **Lilla Karlsö**, precise location unknown, Br41910–29 [30], Br61111–116 [6], **Lilla Karlsö**, precise location unknown, B89141, [32, and 7 unnumbered specimens from the Bather colln., 1909], **Lilla Karlsö** [Basset 90–55], inland locality at scarp rise, halfway between Suderslät and boat landing on SE coast, ca. 5600:3650 [16 spec.]. The Klinteberg locality no longer yields good, abundant specimens, and the precise level at which these were collected in the 19th century is unknown. The best alternative collecting sites are now on the island of Lilla Karlsö, essentially a large Klinteberg reef complex with strata dipping away in all directions (Bassett, personal communication). Bassett and Cocks (1974) report *S. marginalis* also from the Upper

Visby and Högklint beds, but no other *Spirigerina* of that age were found in the Riksmuseet collections.

Spirigerina lockwenia n. sp.

Pl. 24, figs. a–z, ta–tn; Figs. 68–70

1839 *Terebratula imbricata* Sowerby, pl. 12, fig. 12 (right-hand figure only).

1867 *Atrypa marginalis*, Davidson, pl. 15, figs. 1–2.

1882 *Atrypa marginalis*, Davidson, pl. 7, figs. 8, 8a–b.

Name. 'lockwenia' = transposition of the syllables of 'Wenlock', referring to the Much Wenlock Limestone in which it occurs, and Wenlock Edge area where it is most common.

Type locality and stratum. 'Old quarry W Bower's Brook, Benthall Edge Wood' (cited in Sowerby, 1839). This is the locality along Wenlock Edge from which the holotype derives; the largest number of well-preserved and complete specimens come from 'Wenlock Limestone, Tickwood'. The exact horizon of either of these two sources on modern maps is not known: the horizon is probably the upper Much Wenlock Limestone Formation at Wenlock Edge, or lowermost Elton beds (Much Wenlock Lst. at Wenlock Edge, maximal thickness 29 m: Bassett et al., 1975). Thus *S. lockwenia* probably comes from the *ludensis* Zone, of late Homerian, latest Wenlock age. Hurst et al. (1978) concurred that the Much Wenlock Limestone at Wenlock Edge is probably within the *ludensis* Zone. This would agree with the evolution of the *Spirigerina* lineage. The holotype [BB2143, 'Bower's Brook'], and one of the re-discovered paratypes [GSM6601: a figured specimen of Sowerby (1839, pl. 12, fig. 12, right side)], are from the Wenlock Edge area. The latter was labeled by Sowerby (1839, p. 625) as '*Terebratula imbricata*', with the remark, '*T. marginalis* is probably the same species'. This identification by Sowerby is incorrect. *Spirigerina lockwenia* is most common along Wenlock Edge, but scarce in the Dudley area. Its occurrence suggests

Fig. 68. *Spirigerina lockwenia* n. sp. Statistical comparisons of all specimens from Wenlock Edge, Much Wenlock Limestone, latest Wenlock; camera lucida drawings of immature and mature specimen.

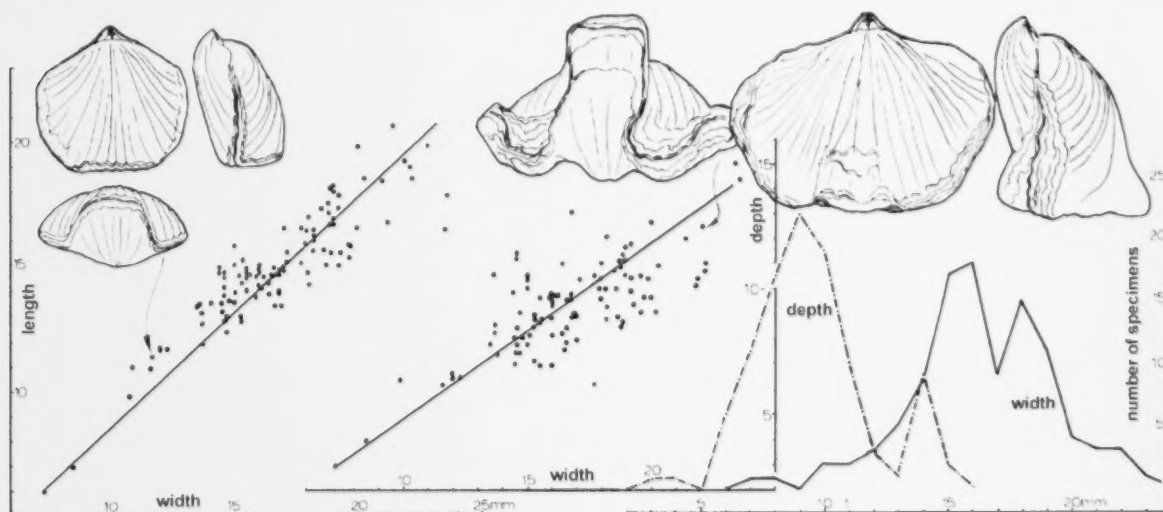
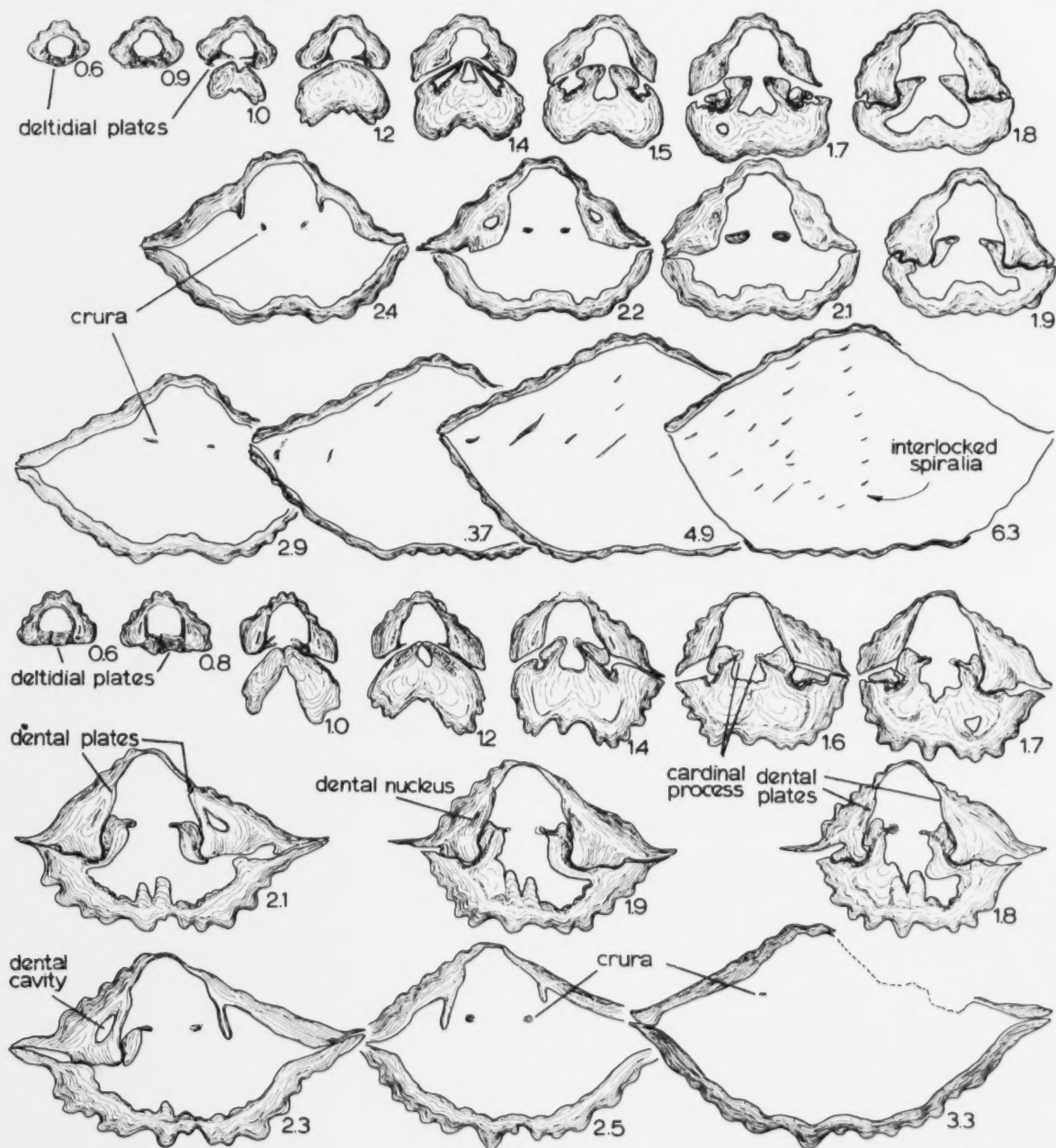


Fig. 69. *Spirigerina lockwenia* n. sp. Serial sections of two specimens; *above*, hypotype BB34776, 'Wenlock Limestone, Tickwood', with interlocked spiralia; *below*, specimen missing spiralia, jugal processes, hypotype BB24119, 'Wenlock Limestone, Dudley', latest Wenlock. Note slit-like dental nucleus, 'dental plates', relatively thin socket plates, prominent inner socket ridges in both specimens; $\times 5$.



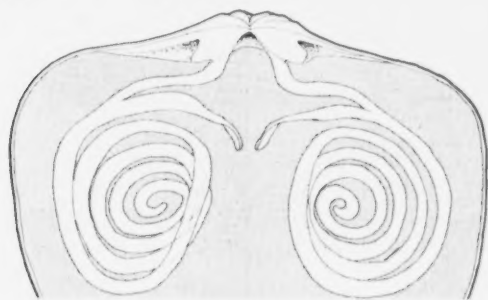
it was a patch reef dweller in the late Wenlock in mid- to outer shelf settings.

Diagnosis. Medium-sized shells, slightly wider than long; vv carinate posteriorly and resupinate anteriorly; dv moderately convex; shell margin surrounded by distinct, dorsally up-turned lip in most shells; protruding apsacline to nearly orthocline area; about 18–25 ribs expanding to commissure; arcuate, ventral mid-rib pair inflated, forming V defining fold;

dorsal fold crest defined by mid-rib pair splitting into 4–6 faint ribs; dorsal fold strong, squared.

Description. Shells averaging 14–18 mm wide, maximum width 23 mm, wider than long, length 13–15 mm, averaging 14 mm long, depths averaging 8–10 mm; rounded outline, dorsibiconvex; vv with marked posterior keel; weakly resupinate along margins; dv moderate to more strongly convex, to inflated in gerontic stages; beak protruding; orthocline to

Fig. 70. *Spirigerina lockwenia* n. sp. Reconstruction from serially sectioned specimen, with well-preserved spiralia, jugal processes, A26666, 'Tickwood, Much Wenlock Limestone', latest Wenlock; $\times 5$.



moderately apsacline area; apical foramen; deltidial plates prominent, with lip; shoulder line indented; dorsal fold distinct, squared U-shape, high, with marked deflection of commissure; distinct brim or lip formed around commissure; ribs long, continuous, expanding anteriorly in size; vv with strong, elevated mid-rib pair diverging, bifurcating distally to flank margins of ventral sulcus; 3–5 finer ribs in sulcus with 2 apical lateral ribs bifurcating to 5–7 ribs; dv with central mid-rib bifurcating to 3–5 ribs on dorsal fold crest; wide rib trough on each side accentuating dorsal fold; short growth lamellae not uncommon on mature shells; lamellae overlapping, crowded, and slightly upturned on dv, downturned on vv, producing brim or flange on which ribs commonly fade. Internally, shell wall thick umbonally, with relatively thick pedicle callist; vv with small dental cavities enlarged anterior to tooth insertion; strong, short, dorsally directed teeth with lateral lobes; deltidial plates short, hollow, opening laterally and anteriorly; dv with minute, striated cardinal process; deep notothyrial pit; bulbous inner socket ridges; crural bases rounded; small crura; jugal processes incurved centrally; spiralia ca. 7 whorls, dorsally directed.

Remarks. *Spirigerina lockwenia* is readily distinguished from *S. marginalis* (Dalman, 1828) by its fewer, coarser, distally expanding ribs (see rib counts), its wide commissural lip and straight, squared ventral fold. Also, the mid-rib pair on the ventral keel is expanded and made of only two, or sometimes four, ribs, but not the large number seen in older *S. marginalis* from Gotland. *S. lockwenia* is intermediate in rib configuration between *S. marginalis* and *S. costata*, which suggests that it lies stratigraphically between the two, i.e., in the upper part of the Klinteberg Limestone and lower Hemse beds on Gotland. The presence of *S. lockwenia* may be used to define the upper limits of the Wenlock in the area.

Materials. Total 134 specimens from the Much Wenlock Limestone in Britain. The species was not found on Gotland. Locus typicus, 'Old Quarry W Bower's Brook', BB2143-48 [holotype and 5 others]; 'Wenlock Limestone, Wenlock Edge', BB108, BB107 [2 specimens from the 'Sowerby, 1839 collection in the BMNH']; 'Tickwood, Wenlock Limestone' A26658-66 [16 shells including multiples on two small slabs], BB34776 [14], BB55167-9 [6 shells, including slab], BB55173-76 [4], BB55178 [1], BB55189-90 [2], BB55199, BB55205, BB55211 [3]; 'Quarry in Tickwood in 600' contour', BB90737, BB90739, BB2149 [3]; 'Wen-

lock Edge, Wenlock Lst.' GS12169-79 [11], GS6601 [figured by J. de C. Sowerby 1839, pl. 12, fig. 12, right side], BB107-8 [3]; 'Wenlock Lst., Salop' BB99 [1], 'Wenlock Lst., Wenlock' A26672-3 [2], A26658-66 [8]; 'Benthall Edge, Wenlock Limestone', B9868 [2]; 'Shadwell Rock Quarry' BB90708 [1]; 'Lincoln Hill, Wenlock Limestone' BB83195-9 [5]; 'Lincoln Hill, N of Iron Bridge', BB90847 [1], BB90828 [1]; 'Dudley, Wenlock Lst.' [probably Upper Quarried Limestone], BB8610 [1], BB24118-9 [4], BB24047 [2], BB24119 [2], A26670 [1], A26667 [1], A26615-8 [3], A26619-34 [19]; locality ?B80415 [1], BB55307-10 [4]; 'Dudley and Walsall', B8048, B 70209, B70210 [3]. This species is represented in numerous museum collections from Wenlock Edge, and its cited abundance herein is not a true indication of real abundance.

Spirigerina costata (Lindström, 1861)

Pl. 25A, figs. a–o; Fig. 71

1861 *Atrypa marginalis* var. *costata* Lindström, p. 363 [short, clear description, but no figures].

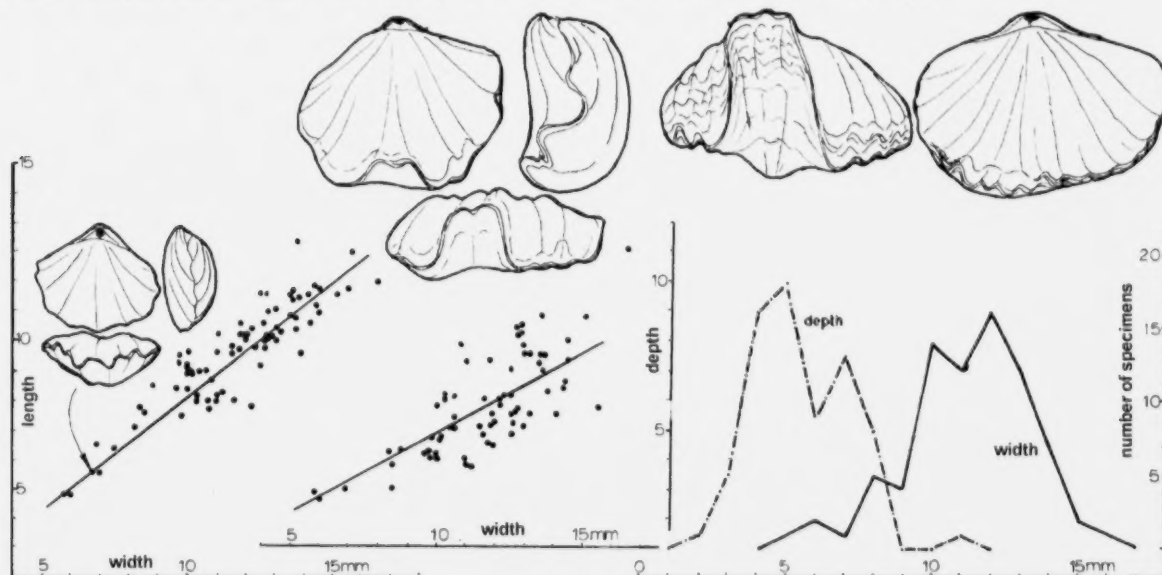
?1878 *Rhynchonella psittacus* Haupt, figs. on p. 70, pl. 2, 12a–f.

Type locality and stratum. Lindström (1861) referred to its occurrence at several localities such as 'Mallgards klint, på Sandarve kulle . . . Linde, Løjsta . . . Etelhem'. Thus a restricted type locality is herewith designated where these are the most abundant in collections, namely 'Sandarve Kulle, Fardhem sn., Hemse beds'. This refers to **Sandarve 1** (Laufer, 1974), the NNE part of the inland cliff, about 1500 m NNE of Fardhem church [4007 5157]. The species was also employed in collections and geological field guides of Munthe, Hede, and von Post (1925a). Munthe, Hede, and Lundqvist (1927) list the species as part of the fauna of the Hemse beds. The level is the upper part of the Hemse beds, *leintward-insens* Zone, early Ludfordian, middle Ludlow. At the type locality and elsewhere, the species is normally associated with or found directly within reefs, in greenish or yellowish brown micrites or shaly pockets. Bassett and Cocks (1974, p. 30) mentioned the existence of a specimen, B88005, from the Bather Gotland collection which fits into this species.

Diagnosis. Shell wider than long; relatively large, moderate to strongly apsacline beak; apical foramen; large deltidial plates; 10–13 highly arched, broadening ribs; dorsal mid-rib pair forming narrow, sharp, anterior fold.

Description. Shells medium sized, 10–15 mm wide, distinctly wider than long, weakly ovoid laterally; dorsibiconvex to planoconvex; ventral valve not uncommonly slightly resupinate at margin due to highly arched ribs, shoulder line deeply indented, arcuate; beak prominent, protruding, moderate to strongly apsacline in adult shells; large apical foramen; deltidial plates touching medially, with lip; 10–15 strong ribs, averaging 12, rounded over most of shell, angular at commissure, expanding rapidly to commissure, bifurcated-trifurcated, rectilinear to curved laterally; single short rib between ventral-mid-rib pair forming fold; dorsal fold formed by single mid-rib, bifurcating near commissure; growth lamellae absent, except at commissure where over-

Fig. 71. *Spirigerina costata* (Lindström, 1861). Statistical survey of specimens from all localities in the middle-upper Hemse beds, early Ludlow; depth peaks at 5 mm, 7 mm; width peak 10–13 mm. Camera lucida sketches of typical specimens.



lapping, crowded; anterior fold narrow, U-shaped to pinched. No serial sections made.

Remarks. Lindström (1861) described the coarse bifurcating and trifurcating ribs of this form [giving a 'rhychonellide' appearance at the commissure], which he said was also smaller than *marginalis*, and called it *Spirigerina marginalis* var. *costata*. This is supported by the collections available (see statistical survey, Fig. 71), which also suggest this shell is generally wider than long, with a longer hinge than other Gotland species. Munthe et al. (1925a, 1927b, 1929) cited the relatively widespread but not abundant occurrence of this species in the Hemse beds on several map sheets. Except at the type locality, *S. costata* is a relatively scarce component in much of the Hemse beds, and it occurs almost exclusively in the reefal facies of the Hemse. It sometimes appears with the smooth atrypoid *Atrypoida hemsea* in reef settings, e.g., at Ljugarn (see Watkins, 1975). The species is readily distinguishable from both *S. marginalis* and *S. lockwenia* by its 'considerably larger and coarser ribs' (Lindström 1861, p. 363), and is closer to *S. quinquecostata*, from which it differs in having almost twice as many ribs, but in ribs which are similarly expanded laterally. The apsacline nature of the beak and foramen indicates strong, probably short adult pedicle attachment in a vertical or suspended position, as the two umbones form a flat resting site. The presence of strong growth lamellae at the commissure of a few specimens may give the misleading superficial impression of resemblance to *Xanthea*. However, early growth stages of the shell show smooth, continuous ribs with a micro-ornament typical of *Spirigerina*. From Silurian erratics in Germany, Haupt (1878) described a *Spirigerina* which he called '*Rhychonella*' *psittacus*. The relatively coarse *Spirigerina*-like ribs suggest it is an atrypid but that it can be neither *Spirigerina marginalis* nor *S. lockwenia*. It is probably *S. costata* from the Hemse beds of Gotland. However, this species has been forgotten in

the literature, and the types cannot be traced, leaving its identity doubtful.

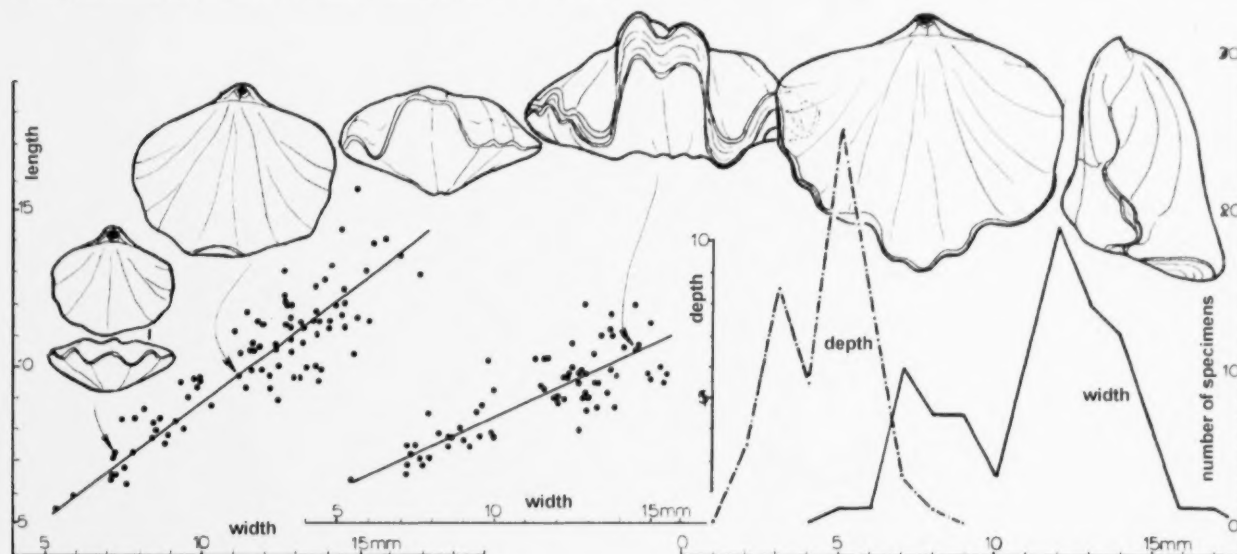
Materials. Total 95 specimens, all from the Hemse Formation. '**Sandarve Kulle**', type locality, Br42071-133, Br107506-11, Br108047 [71 shells]; '**Linde Klint**, O-sidan' Br46821-27 [7]; '**Marmorbröttet**, vid **Tänglings V** om järnvägen', quarry, Br104656-58 [3]; '**Ljugarn 1**, shoreline outcrop around patch reef [SW38: 3]; '**Tänglings 4**, road outcrop 2 km S Etelshem, reefal Hemse beds [SW34: 5]. Lindström (1861) also cited **Mallgårds Klint**, **Etelshem**, and **Lojsta**, but this material could not be found in collections.

Spirigerina quinquecostata (Munthe, 1911)
Pl. 25B, figs. a-r; Figs. 72, 73

- 1911 *Atrypa marginalis* var. *5-costata* [sic] Munthe, p. 1418, figs. 16a-b.
1921 *Atrypa marginalis* var. *5-costata*, Munthe, figs. 13d (1-2).
1960 *Plectatrypa marginalis quinquecostata*, Hede, p. 84 [used the fully spelled name for the first time].

Type locality and stratum. '... upper strata of Hoburg ... confined to the southernmost and southeast parts of the area in question' [south Gotland: Munthe, 1911], and 'younger crinoid limestone' (ibid., p. 1417), i.e., Hamra Formation, units B-C, ca. *formosus* Zone, Ludfordian, late Ludlow [no graptolites are known to be associated with these]. Jeppsson (1983) suggested that the uppermost units on Gotland may be younger than the upper Ludfordian of the type area in England. The species from Hoburg was described by Lindström (1861, p. 363), but not formally named, as 'i några exemplar erhållits från Hoburg, men hvilken på dorsaskalet ej har mer än fem grofva, starkt upphöjda tvåklufna costae och påa ventralskalet sex' [transl., 'a few specimens have been

Fig. 72. *Spirigerina quinquecostata* (Munthe, 1911). Statistical analysis of a single nest of specimens from Hoburgen 2, late Ludlow; typical specimens in camera lucida sketches. Bimodal peaks suggest a 2-year recruitment phase, and possible rates of shell growth over 2-year period: depth peaks at 3, 5 mm, width peaks at 7, 12 mm.



extracted at Hoburg, but the dorsal valve has no more than 5 coarse, strongly raised bifurcating costae and on the ventral valve six']. I found that the species occurs abundantly in green shaly pockets adjacent to and within coral-stromatoporeid reefs, and in crinoidal limestones at the northern small bluff directly south of Hoburgsgubben (see **Hoburgen 2**), which can be regarded as the locus typicus restrictus [CJ 4140 1285; 51 Hoburgen SO 12960:41340]. Hede (1960, p. 84-86) described the Storborg locality at Hoburgen in some detail, citing '*Plectatrypa marginalis quinquecostata*' from pockets within the patch reefs, but the Hede collections could not be found. A neotype, Br106550, is selected from the specimens figured herein, as no types were designated. Munthe (1911), following the description of Lindström (1861), only described the typical five ribs on the vv, and provided a photograph of a specimen (this specimen was not located), but it is clear where the specimen was collected, and what it looks like.

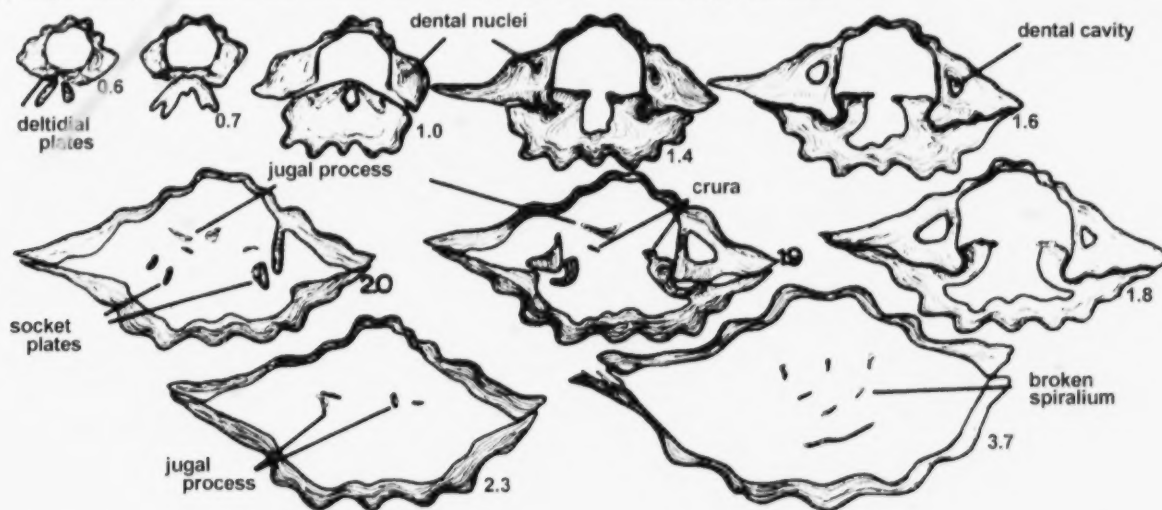
Diagnosis. Small to medium sized (11-14 mm wide), wider than long; apical foramen, triangular deltidial plates; prominent, protruding beak; orthocline to slightly apsacline area; distinct W-shaped fold flanked by strong, divergent, ventral mid-rib pair; single weak anterior rib on smooth ventral tongue; vv with 5-7 ribs; dv 6-8 ribs; anterior fold sharp, W-shaped.

Description. Shell usually wide, relatively flat; width greater than length; average 11-13 mm wide, maximum 17 mm; average 9-11 mm long; depths 4-6 mm, averaging 5 mm; vv keeled but relatively flat; dv weakly to moderately convex; beak protruding, prominent, commonly subtriangular; neanic apsacline area, weakly apsacline-orthocline adult shells; foramen oval to round, apical; small triangular, lipped deltidial plates exposed; shoulder line deeply indented, curved; apical angle 110°-130° for widths less than 10 mm, 130°-155° for large shells. Ribs strong, usually 5 on vv, 6 ribs on dv;

gerontic specimens displaying highly upwardly curved, raised, expanded ribs and fold on dv, almost forming flange; ribs continuous, curved laterally, expanding distally, tubular, rarely interrupted by any but faint growth lamellae; where preserved, distinct microfilae and radial ridges on crests and troughs; ventral mid-rib pair prominent, forming keel, laterally expanding to accommodate fold; lateral ribs less prominent, fading to sides; dv with small mid-rib bifurcating at commissure at fold crest, 3-4 lateral ribs; shell wall with overlapping growth lamellae around commissure forming shell closure; fold W-shaped, strong, angular. Internally, very thin or no pedicle callist; deltidial plates triangular, prominent, solid to slightly hollow, but open where wrapped around dorsal umbo; teeth blunt, solid apically; faint trace of elongated dental nucleus, opening into large, rounded dental cavity anteriorly; teeth with weak lateral lobes; small cardinal pit expanded distally into bilobed space divided by stout dorsal septum; hinge plate thickened around inner socket ridge; weak outer socket ridge; crural bases small, delicate; short, unfeathered, horizontal crura; jugal processes thick, relatively massive; only broken, disjointed spiralia observed inside sectioned specimens.

Remarks. This is the youngest species in the *Spirigerina* lineage on Gotland. It is easily distinguished by the presence of its relatively few, large, expanding ribs [hence the name], and distinctive shape from all other species on the island. This distinction was mentioned by Lindström (1861), who stated the dorsal valve has only five strong, elevated bifurcating ribs, and the ventral valve six. However, larger specimens commonly have up to 7-8 ribs on either valve. Rare specimens of *Spirigerina costata* from the Hemse beds, usually have about twice the number of ribs per shell, but small specimens approach, but not equal, *quinquecostata* in its limited rib number and in expanding rib size. The fewer ribs were probably derived neotenously. It comes closest to *Spiri-*

Fig. 73. *Spirigerina quinquecostata* (Munthe, 1911). Serial sections, paraneotype Br106553, from Hoburgen 2, late Ludlow; note relatively large distally expanded dental cavities, damaged spiralia, and dislocated jugal processes; $\times 5$.



gerina marginaloides (Nalivkin 1926, in Rzhonsnitskaya, 1975) in its loss of ribs, but differs from that species in its distinct ventral-mid-rib pair and fold. The general evolutionary trend towards rib coarsening in *Spirigerina* from the Baltic demonstrate that the subgenus *Neospirigerina* cannot be distinguished here, unless internal criteria are different (see Rzhonsnitskaya, 1975). The fine micro-ornament seen under SEM is well preserved in many specimens (Fig. 4e; Pl. 25B, figs. q, r). It is similar to that seen in the type species of the

genus, *Spirigerina marginalis*, but also has a radial component not seen in the latter.

Materials. 134 specimens, all from the Hamra Fm. Locus typicus restrictus, **Hoburgen 2**, or 'Hoburgsgubben', at or near the original type locality, single small reef pocket, <1 cubic metre [SW35: 122 shells]; '**Hoburgen**, V-sidan', Br108062-3 [2], Br108066-69 [3], Br108071-76 [6]. **Hoburg**, Br88725-35 [11].

Superfamily Lissatrypoidea Twenhofel, 1914

Family Lissatrypidae Twenhofel, 1914

Subfamily Lissatrypinae Twenhofel, 1914

Remarks. The main characteristics of the Lissatrypinae, other than the smooth shell, are the thick, solid, and relatively massive hinge plates and teeth without dental cavities. Internally, the spiralia are dorsally oriented and jugal processes disjunct. Beaks tend to be small, incurved, and obscured, usually developing deltoidal plates only in earliest growth stages. A pedicle opening is commonly lost or enlarged through the ventral umbo. Johnson and Boucot (1970), followed by Sheehan (1982), divided the smooth atrypoids into two groups based on the presence or absence of 'inner hinge plates'. This is not verifiable in sectioning species of smooth atrypids, as the hinge plates are usually not definable into outer and inner portions, nor in microstructure of the shell hinge and wall (Copper, 1986). This separation of smooth atrypids would have split off, for example, the genus *Atrypoidea* from the Lissatrypinae, to which they are undoubtedly very close in all aspects of their hinge structures, jugal processes, and spiralia, and would have lumped the Septatrypinae with the ribbed genus *Atrypa*, with which they have nothing in common externally and internally, except for orientation of spiralia. A revised view of the Lissatrypidae

genera is shown in Copper (1986, 2001a, 2002b). Within the Lissatrypinae, the Late Silurian genus *Atrypellina* Menakova and Nikiforova (1986) diverges from others in having a sharp, angular anterior fold, as others are more moderately biconvex. The oldest *Septatrypa*-like form, *Webbyspira*, is now known from the early Caradoc of Australia (Percival, 1991), with the 'septatrypine' *Idiospira* appearing in the late Caradoc (Copper, 1986). Older smooth protozygines (Lissatrypinae) are assumed to exist in the late Llandeilo (Copper, 1996b, 2001a, 2002b).

Meifodia Williams, 1951

Type species. *Hemithyris subundata* M'Coy 1851, Mathryfal, near Meifod, Wales, late Rhuddanian (A3–A4), Llandovery.

Range and distribution. Llandovery, Eurasia, North America. In Western Europe the genus appears to originate in the early Llandovery, declining by the mid-Llandovery. The species '*Meifodia*' *supercedens* (Williams, 1951) probably belongs to *Septatrypa*.

Diagnosis. Small to medium sized, smooth, dorsibiconvex; normally transversely ovoid; incurved beak; small orthocline-anacline area; apical foramen; minute deltidial plates; broad dorsal fold; shell wall relatively thick; thick pedicle callist or collar; solid teeth lacking dental cavities; weak dorsal septum; jugal processes terminating in hook-like jugal plates, dorsally directed spiralia with fewer than 15 whorls.

Remarks. The various British species exist entirely as casts and moulds, for which it is deceptively difficult to assess whether they are athyridids or atrypids. Indeed, *Meifodia* was initially assigned to the Athyridida by Williams (1951). Possibly some may be referred to *Lissatrypa* or *Septatrypa*, but this is uncertain, as the internal structure of the teeth and brachidia in British shells are unknown. The internal description of *Meifodia* has had to be based on well-preserved shells from the Oslo area of Norway, which has clarified the dental structure, hinge plate, jugal processes, and spiralia (Copper, 1995). *Meifodia* externally resembles some *Septatrypa* in having a broad dorsal fold, but internally lacks the large dental cavities, dental plates, and delicate hinge plates of *Septatrypa*. *Meifodia* is clearly related to, and probably ancestral to, *Lissatrypa* in its thick shell with solid teeth, its hinge plates, and lack of dental plates or dental cavities. Williams (1951) mentioned the evolution of a 'septalium' in the later forms, such as *Meifodia supercedens*, which suggests that this species may instead be a *Septatrypa*; however, no mention was made of the presence of dental cavities or dental plates. Dental plates or dental cavities are absent in *Meifodia*, and none were found in specimens examined from Norway, nor the related genus *Cerasina* from Anticosti. Williams (1951) proposed a number of evolutionary modifications of the cardinalia with time, e.g., the septum: since some of these were related to the end species of the lineage, which is probably a *Septatrypa* (see *S. supercedens*), these changes are cross-generic and do not reflect an evolutionary lineage. The late Rhuddanian genus *Cerasina* Copper 1995 from Anticosti Island resembles *Meifodia* in its shape and broad, wide anterior fold, but possesses a primitive jugum instead of separated jugal processes. The genus *Tyrothyris* (Öpik, 1953) from Llandovery rocks of eastern Australia, also mistaken for an athyridid, is a junior synonym of *Meifodia*.

Sheehan (1982) suggested that the genus *Meifodia* was a descendant of the finely ribbed catazygine *Pentlandella* by loss of ribs, and that the smooth *Lissatrypa* were therefore completely independent in their ancestry from the smooth *Septatrypa*. Serial sectioning shows that these two genera have nothing in common except a slightly thicker shell wall (also possessed by Caradoc-Ashgill *Idiospira*). The ancestry of *Meifodia* is enigmatic, as it appears suddenly in the post-Ordovician mass extinction recovery on Laurentia and Baltica. *Meifodia*, which first appears almost at the very base of the early Llandovery (Rhuddanian) in Norway is the undoubted ancestor of *Lissatrypa*, which has its first occurrence on Anticosti Island in the late Aeronian Richardson Member of the Jupiter Formation. In Czechoslovakia *Lissatrypa* first appears in the Motol Formation (Wenlock; Havlíček 1984, 1990). Both genera share similarities in the relatively thick, solid hinge plates and massive teeth. The distribution of *Meifodia* in the British, Norwegian, and Estonian sections suggests that this is a deeper water genus: the

related genus *Cerasina* from Anticosti is similarly also a deeper water genus. Llandovery species of *Lissatrypa* from Anticosti occur initially in deeper water settings of the *Diceloxia* community, then shallow upwards, and only Telychian-Wenlock taxa are found in shallower water, as well as deep water settings.

Species tentatively assigned.

- Meifodia recta alia* Nikiforova 1978, Chasman-Kalon, Altai-Sayan Mtns., Tienshan, Minkuchar beds, Llandovery.
 ?*Septatrypa antiquata* Nikiforova 1961, Moiero River, Siberia, Llandovery [see also Nikiforova, 1954].
 ?*Lissatrypa humanensis* Rong, Xu, and Yang 1974, Shimen-longchi R., Hunan, Xiangshuyuan Fm., late Llandovery.
Septatrypa letnyaensis Lopushinskaya 1976, Tenna-Ses R., near Letnei branch, Siberian Platform, middle Llandovery [see also Lopushinskaya, 1965].
 ?*Meifodia lissatrypaformis* Zeng 1987, Wangjiawan, Yangtze R., Luoropin Fm., Llandovery [possibly *Lissatrypa*].
Septatrypa magna Nikiforova 1961, Siberian Platform, middle-late Llandovery.
 ?*Meifodia orientalis* Rong, Xu, and Yang 1974, Meitaixing-longchang, Guizhou, Xiangshuyuan Fm., Llandovery [possibly = *Lissatrypa*, but shows dental cavities].
Meifodia ovalis Williams 1951, SW of Llwyn-yr-iar, Wales, B3, Aeronian.
Septatrypa magna forma *pentagonalis* Nikiforova 1961, Siberian Platform, Llandovery.
 ?*Lissatrypa recta* Nikiforova 1961, Moiero River, Siberia, Llandovery.
 ?*Glossia obovata sibirica* Kulkov 1989, Inya River Basin, NW Altai, Yavors beds, Aeronian.
Meifodia subundata prima Williams 1951, NW of Scrach, Wales, A3, Rhuddanian.
Hemithyris subundata M'Coy 1851, Mathryfal, near Meifod, Wales, late Rhuddanian, Llandovery.
Meifodia subrotunda Su 1980, Heilongjiang, NE China, Llandovery.
 ?*Atrypoida trapezoidea* Fu 1982, Shaanxi, N China, Llandovery [see also Lin, 1984, pl. 6].

Meifodia cf. *prima* Williams, 1951

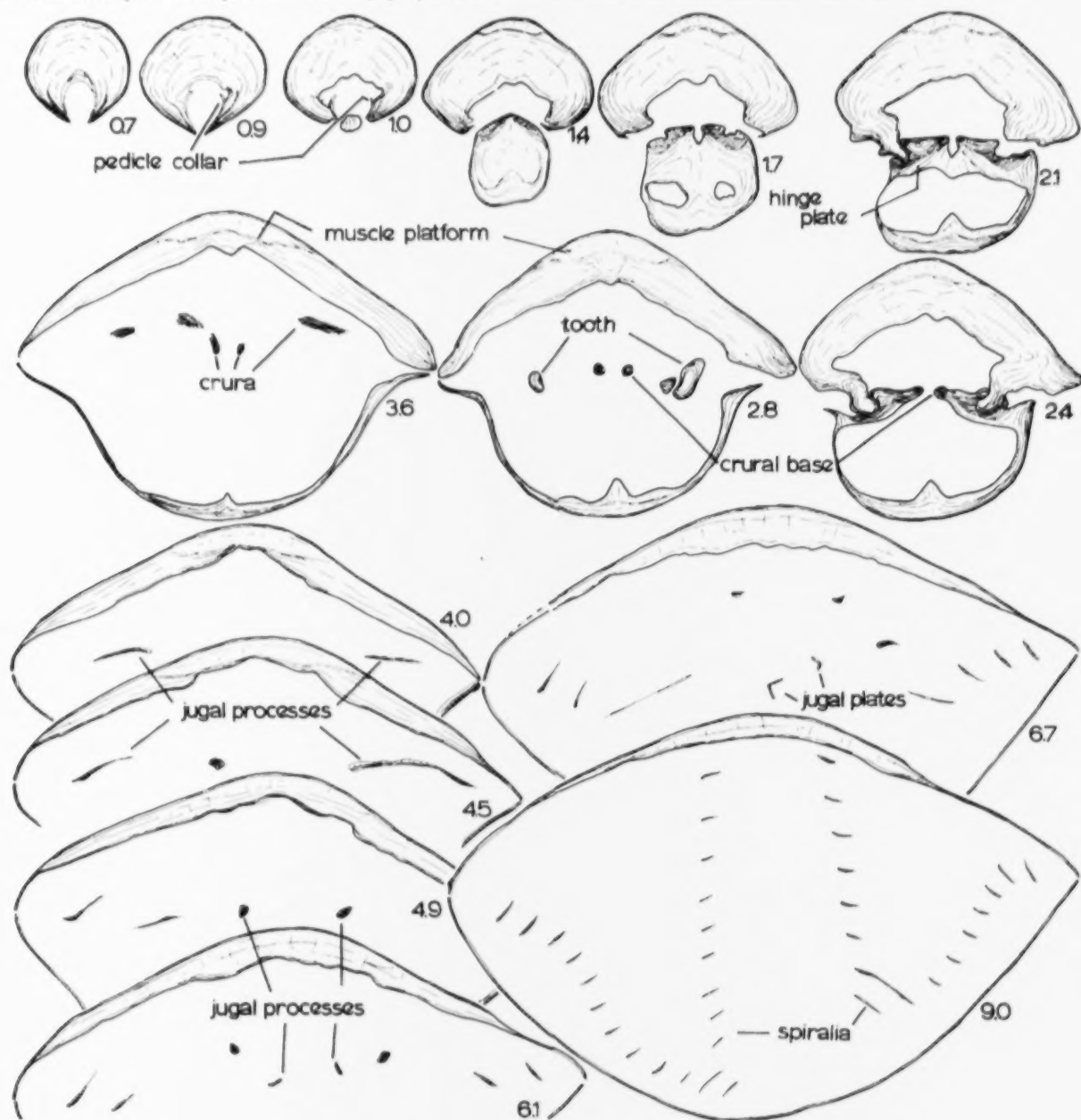
Fig. 74

- 1951 *Meifodia subundata prima* Williams 1951, p. 107–109, pl. 6, figs. 1–3.
 1982 *Meifodia subundata* (M'Coy 1851), Thomsen and Baarli, pl. 3, figs. 7–8.
 1995 *Meifodia* sp., Copper, figs. 14–15.
 2002b *Meifodia subundata* M'Coy 1851, Copper, fig. 993, 1a–g.

Type locality and stratum. . . . a quarter of a mile northwest of Scrach, northeast of Llandovery, Lower Llandovery (A3) (Williams, 1951). In Norway this species, or one very similar to it, ranges down to near the base of the Llandovery, within a few metres of the Ordovician boundary (i.e., base to middle of the Solvik Formation, units 6A–6B).

Remarks. Since British material is not preserved as whole shells, collections were made in Norway in carbonates of early Llandovery age in order to determine the nature of the

Fig. 74. *Meifodia* cf. *prima* Williams, 1951. Serial sections of specimen from the Solvik Fm., Malmoeysa, near Oslo, Norway, Rhuddanian, early Llandovery. Note the small jugal plates at the ends of the jugal processes, thick pedicle callist; $\times 4$.



spiralialia and jugal processes, as well as the hinge plates and teeth. Specimens of the Norwegian species were serially sectioned to confirm their affinity to Lissatrypidae (see Copper, 1995, 2002b). The Norwegian shells, which occur with *Protatrypa malmoeysensis* Boucot and Johnson (1964), tend to be relatively wider than long, are larger than British types, and have a very broad, flat anterior fold. The shell is smooth and undefined by growth lines, but marked by rare growth interruptions near the commissure. These shells were identified by Thomsen and Baarli (1982) as *Meifodia subundata* (M'Coy),

but appear to be different from this British species in shape and can probably be more appropriately assigned to *M. prima* Williams 1951. M'Coy (1851) said that *M. subundata* averaged an inch, or 25 mm in width, and illustrated (M'Coy, 1855, pl. 1h, figs. 9, 9a–c) a large shell of about that size, about the same size as the Norway form. On Anticosti there are no shells of *Meifodia* (nor *Protatrypa*) in the 140 m thick, fossiliferous Beccie Fm. of Rhuddanian age, although other dwarfed taxa of *Cryptothyrella*, *Becciea*, etc., are common at the base of the formation, and large *Virgiana* at the top.

Materials. Total 32 shells from the Solvik Formation, Malmoey, near Oslo, early Rhuddanian.

Lissatrypa Twenhofel, 1914

[= *Spondylobolus* M'Coy, 1851, nomen oblitum; *Loilemia* Reed, 1936; *Nanospira* Amsden, 1949; *Lissatrypoidea* Boucot and Amsden, 1958; ?*Holynatrypa* Havlíček, 1973; ?*Buceqia* Havlíček, 1984; ?*Cromatrypa* Havlíček, 1987; *Solitudinella* Godefroid, 1991]

Type species. *Lissatrypa atheroidea* Twenhofel 1914, west side mouth of Jupiter River at Bonsecours Creek, Anticosti, Canada, Jupiter Fm., upper Richardson Mbr. [corrected from Copper, 1973a], late Aeronian (*Stimulograptus sedgwickii* Zone), Llandovery.

Range and distribution. Worldwide, middle Llandovery–Emsian, ?early Eifelian.

Discussion. [For diagnosis see Copper, 1973a, Copper, et al., 1988; Copper, 2002b.] It should be noted that small shells may have an apical foramen flanked by deltidial plates, but in most adult shells the foramen is transapical with an internal pedicle callist leading to small collar, and the beak is incurved, obscuring the deltidial plates and foramen. The hinge plate is thick, raised medially and normally, but not invariably, lacks a medial cardinal pit in adult or gerontic shells. Inner socket ridges tend to be bulbous. The exterior of the shell is commonly smooth, but may also be covered by concentric layers of fine, fibrous crystals forming a spinose coating of the shell. This is often worn away during life or post-mortem, even when no sign of wear is evident.

Lissatrypa is one of the most widely misidentified atrypoid genera, probably because its smooth shape leaves few identifying characters. The genus is commonly mistaken for athyrids, or even inarticulates. A large number of genera have been separated from *Lissatrypa*, but the internal structure of these is the same, and they are junior synonyms, with purported differences based on minor external shape variation, or misinterpretation of internals. Conversely, a number of other smooth atrypids, mostly *Atrypoidea*, [e.g., from Gotland] have been misidentified as *Lissatrypa*. *Lissatrypa* is thus far unknown on Gotland, although it is present in Britain and Estonia. The name *Spondylobolus* was not formally used in more than 150 years, and is regarded as a nomen oblitum, although it has priority over *Lissatrypa*. Salter (1873, p. 139) was the first to recognize *Spondylobolus craniolaris* as a junior synonym of '*Meristella*' [= *Lissatrypa*] *obovata* Sowerby 1839, and determined it as coming from the Wenlock Shale. Cocks (1978) revived the idea that *Spondylobolus* was a crushed shell of *Atrypa obovata*, the type species of *Glassia* Davidson 1881 (see Copper, 1996b, 2001c, and herein, for a revision of *Glassia*). To resurrect the genus name *Spondylobolus* would create considerable confusion, as the genus *Lissatrypa* has given its name to the suborder, superfamily, family, and subfamily. The type species of *Loilemia* (Reed, 1936) from northern India is based on partly preserved moulds preserved in a friable sandstone; no other specimens have been described and this form very likely belongs to *Lissatrypa* [personal examination, Reed collection, Geological Survey, Calcutta, where the type specimen re-

sides]. The internal and external structure of *Nanospira* and *Lissatrypoidea*, two genera described from the southeastern U.S. (Amsden, 1958b), are indistinguishable, and identical to *Lissatrypa* (Copper et al., 1988). The North African (Morocco) Devonian genus *Solitudinella* cannot be distinguished from its North American *Lissatrypoidea* (= *Nanospira*) counterparts either internally or externally (young or dwarfed shells of *Lissatrypa* are also dorsibiconvex through planoconvex, and ligate shells are common).

Lissatrypa is readily distinguishable internally from *Glassia* by its dorsally oriented spiralia (instead of medially directed spiralia), pedicle callist, and solid teeth lacking dental cavities or dental plates. The muscle scars of *Lissatrypa* tend to be small and deeply incised into the thick shell. Externally, the genera may be similar: *Lissatrypa* has a rounded shell with a transapical foramen through which a small collar is normally visible. The *Glassia* shell is elongate, with a pointed, anacline area (foramen lacking a collar); the shell commissure is usually, but not always, distinctly bisulcate (accommodating the medial spiralia internally). *Glassia* also lacks any sign of external fibrous needles (the 'furry coating' of the primary layer), as seen in pristine *Lissatrypa*. *Glassia* is present in both Gotland and Britain. *Lissatrypa* is unknown in Gotland, although common in the Llandovery–Wenlock of Latvia at the east end of the Baltic Basin (Rybnikova, 1967; Brazauskas and Musteikis, 1991; Musteikis and Juskute, 1999; Musteikis and Paskevicius, 1999), and in Podolia (Venjukov, 1899; Kozłowski, 1929; Nikiforova, 1954; Modzalevskaya, 1968; Tsegelnyuk, 1976; Modzalevskaya and Nikiforova, 1982; Nikiforova et al., 1985).

Havlíček (1984) compared *Buceqia*, with dorsally directed spiralia, to the genus *Cryptatrypa* (Siehl, 1962), a junior synonym of *Glassia*, with medially directed spiralia and imbedded dental plates. However, the serial sections shown by Havlíček for the type species of *Buceqia*, *Terebratula obovata* Barrande 1847, are those of a typical *Lissatrypa* shell. The type species of *Holynatrypa* (Havlíček, 1973), an Eifelian form, is possibly also a synonym of *Lissatrypa*, and if so, the youngest known. It was said to have 'spiralia probably directed medially', but this was never illustrated, and its internal structure and affinity are uncertain; it could be a glassiid. The Ludlow genus *Cromatrypa* (Havlíček, 1987) is a very small, less than 8 mm wide, smooth atrypoid of uncertain affinities: in serial sections shown by Havlíček (1991), it resembles *Lissatrypa*. *Cromatrypa* is said to possess a small foramen and deltidial plates, which Havlíček believed sufficient to distinguish it from *Lissatrypa*. However, *Lissatrypa* also has a foramen flanked by deltidial plates, although often obscured under the hypercline umbo (Copper, 1973a).

Xu (1979d), using moulds and casts, believed that it is possible to separate the smooth shells of *Holynatrypa*, *Nanospira*, *Australina*, *Lissatrypoidea*, and *Glassia* on the basis of muscle scars and septal development. This is clearly untenable. *Nanospira* and *Lissatrypoidea*, described from the U.S., are synonyms of *Lissatrypa*. *Glassia* has distinctive medially oriented spiralia, but muscle scars are similar to those of *Lissatrypa*. The Chinese smooth atrypinine *Gracianella* (*Guangyuania*) Sheng 1975 (Aeronian, Sichuan) is similar to *Lissatrypa* in sharing an external primary layer made up of radial fibres. However, the prominent orthocline area, exposed deltidial plates, and early carinate, ribbed growth

stages indicate that *Guangyuania* is like smooth varieties of the carinatinine *Gracianella*, showing adult rib loss. The genus *Claratrypa* (Havlíček, 1987) was designated for smooth species previously assigned to *Gracianella*; thus *Guangyuania*, like *Gracianella* s.s., spans all these variations from ribbed forms such as *Gracianella* (*Sublepidia*) Mizens and Sapelnikov 1982 to smooth species.

Lissatrypa has a wide distribution and long geologic record. The ancestry of *Lissatrypa* probably lies with early Llandovery *Meifodia*, which has the thick shell wall of *Lissatrypa*, circular outline, and small pedicle opening. From the outside, *Lissatrypa* lacks a fold or has only a weak sinuous dorsal fold, whereas *Meifodia* normally has a broad, squared fold and wider, more inflated shell. Internally, *Lissatrypa* has highly rounded, inflated, and fused hinge plates, with virtually no cardinal pit, forming a bulbous type of 'cardinal process', used for attachment of diductor muscles: it is the only atrypid genus known to have this structure, although some *Atrypina* also lose a cardinal pit. The type species of *Lissatrypa* is perhaps the oldest species in the genus, as it occurs in late Aeronian strata of the Richardson Mbr. (Jupiter Fm.) on Anticosti Island. The genus '*Glassia*' has been widely reported from many British sections, and commonly has been cited an indicator species for specific communities. For example, '*Glassia*' is said to be present within the Llandovery 'isorthisid-*Glassia*' community (Tipper, 1975), *Dicelosisia* community (Kaljo and Klaamann, 1982), within the Wenlock deep water *Vishyella* community, and shallow water *Sphaerirhynchia* community (Fürsich and Hurst, 1974; Hurst, 1975), and in the early Ludlow, somewhat deeper shelf '*Glassia obovata*' association of the Welsh Borderlands (Watkins, 1979). However, virtually all the specimens identified by this name are assignable to *Lissatrypa*, and these benthic assemblages must be renamed.

Species tentatively assigned (41 species listed, including many questionable taxa without internal data, 4 with identical species name; 10 species were named by Havlíček from the Prague Basin alone).

- Lissatrypa baterobaoensis* Su, Rong, and Li 1985, Bateobao, Inner Mongolia, Bateobao Fm., Ludlow.
Lissatrypa cibia Havlíček 1984, Prague Basin, Lodenice-Luzce, Motol Formation, Wenlock [= ?*craniolaris*].
Nucleospira clairensa Thomas 1926, Batesville, Arkansas, Clarita Fm., Fitzhugh Mbr., late Wenlock.
Atrypa compressa Sowerby 1839, Woodside and Nash, Presteigne, 'Wenlock Shale', middle Wenlock.
Lissatrypa compressiformis Mizens 1977, N Urals, Kolonga River, Striatov Horizon, Ludlow.
Nucleospira concentrica Hall 1859, Decatur, Tennessee, Brownsport Fm., Ludlow.
Spondylobolus craniolaris McCoy 1851, Builth Bridge, Powys, Wenlock Shale, Wenlock.
? *Holynatrypa crucifera* Havlíček 1973, Prague Basin, Trebotov beds, Emsian-Eifelian.
Cryptatrypa curvirostris Xu 1979d, Guangxi, Tangxiang Formation, ?Emsian-Eifelian.
Lissatrypa decaturensis Amsden 1949, Blue Mound Glade, Tennessee, '30–45 ft.' above base of Brownsport Fm., Ludlow [= junior synonym of *L. concentrica* Hall, 1859].

- Buceqia elliptobola* Havlíček 1991, Prague Basin, Listice, Motol Fm., Wenlock.
Lissatrypa fumida Havlíček 1984, Prague Basin, Kozolupy, Kopanina Fm., early Ludlow [= ?*Lissatrypa obovata*].
Lissatrypa henryhouseensis Amsden 1951, Ada, Oklahoma, Henryhouse Fm., Ludlow.
? *Lissatrypa hoboksarensis* Zhang 1981, Hoboksar, Dzungar Basin, NW China, Shabareti Fm., Wenlock.
Lissatrypa hypercincta Havlíček 1984, Prague Basin, Koneprusy, Koneprusy Lst., Pragian – early Emsian.
Atrypella inflata Fang 1974, Qujing, eastern Yunnan, Miaokao Formation, Late Silurian.
Lissatrypa jucunda Oradovskaya 1975, Yasachnoi River, Malovodny Creek, Anikins Suite, Telychian, Llandovery.
Lissatrypa kazakhstanica [sic] Borisov 1955a, Karagandinsk region, Kazakhstan, Wenlock.
Lissatrypa lenticulata Philip 1962, Tyers, Victoria, Australia, Boola beds, ?early Pragian.
Lissatrypa leprosa Kozłowski 1929, Ustye, Podolia, Ukraine, Borshchov Fm., Lochkovian.
Lissatrypa lithuanica Paskevicius, Modzelevskaya, and Musteikis 2002 (in Musteikis and Modzelevskaya, 2002), borehole material, Lithuania, Riga Fm., Wenlock.
Glassia minuta Rybnikova 1967, Kholdre, Latvia, Telychian (series by Rybnikova, 1985, indicate *Lissatrypa*: see also Kulkov, 1978 for Tuva material).
Lissatrypa minuta Kulkov 1967a, Ini River, NW Altai, Chagyr beds, Wenlock.
Glassia minuta Fu 1982, Qinling Mountains, China, ?Wenlock-Ludlow.
Lissatrypa minuta Doyle, Harper, and Parkes 1990, Ireland, Tonalee Formation, Telychian, Llandovery.
? *Holynatrypa mirabilis* Xu 1979d, Guangxi, Tangxiang Fm., ?Emsian.
Lissatrypa neglecta Havlíček 1984, Prague Basin, Praha-Reporýje, lower Lochkov Fm., early Lochkovian.
Terebratula nuda Eichwald 1840, Bogoslovsk, Urals, Ludlow.
Terebratula obolina Barrande 1847, Prague Basin, Kozle, Motol Fm., late Wenlock [type species of *Buceqia*].
Atrypa obovata Sowerby 1839, Wenlock Edge, U.K., Much Wenlock Limestone, late Wenlock.
Lissatrypa operosa Kulkov, 1967a, Chergi River, central Altai, Kunmov Suite, Ludlow.
Australina orientalis Su 1976, Bateobao, Inner Mongolia, Xibiehe Fm., Ludlow.
Nanospira parvula Amsden 1949, Chimneyhill Creek, Oklahoma, Henryhouse Fm., Ludlow.
Lissatrypa philomelaformis Mizens 1977, E slopes central Urals, Vya River, Striatov Horizon, Ludlow.
Lissatrypa postfumida Havlíček 1991, Prague Basin, Praha-Reporýje, Kopanina Fm., late Ludlow.
Cromatrypa? pubes Musteikis and Modzelevskaya 2002, Lithuania, borehole material, Rusne Fm., early Ludlow.
Glassia rotunda Rybnikova 1967, Piltene, Latvia, middle Ludlow [Havlíček assigned this to *Cromatrypa*].
? *Lissatrypa sarburtensis* Zhang 1981, Dzungar Basin, NW China, Shabareti Fm., Wenlock.
Glassia obovata sibirica Kulkov 1989, Inya River, Altai Mountains, Llandovery.

Lissatrypa sigillata Havlíček 1984, Prague Basin, Praha-Barrandov, Dvorce-Prokop Lst., Pragian.

?*Glossia tenella* Williams 1951, SSW of Cwm Crychan, NE of Llandovery, Wales, Aeronian, Llandovery.

Terebratula turjensis Gruenewaldt 1854, Vagran River, E slopes Urals, Karpinskii Horizon, middle Emsian.

Glossia variabilis Whitcaves, 1904, Hudson Bay, Winisk River, Ontario, Ekwon River Fm., Telychian, Llandovery.

Lissatrypa villosa Havlíček 1984, Prague Basin, Praha-Klukovice, Reporyje Lst., Pragian.

Lissatrypa cf. *minuta* (Rybnikova, 1967)

Pl. 26A, figs. a-l; Figs. 75, 76

?1899 *Glossia obovata*, Venyukov, pl. 1, fig. 21 [Podolia, Studenitza].

1967 *Glossia minuta* Rybnikova, p. 203-204, fig. 33, pl. 23, figs. 3a-d.

[non *Lissatrypa minuta* Kulikov 1967a, non *Glossia minuta* Fu 1982]

Type locality and stratum. Kholdre, Latvia, Telychian (Rybnikova, 1967). In Britain this occurs on the south bank of Harley Brook, '270 yards SW Domas', SJ 5936:0062, 'locality 134' (Whittard), near Wenlock Edge, Hughley Shale, late Llandovery, Telychian. The probable facies is a distal ramp or slope, deep water setting.

Diagnosis of British material. Small biconvex, rounded *Lissatrypa*, averaging 5-6 mm wide, 2 mm deep.

Description (British material). Highly rounded outline; usually wider than long, widths averaging 5-6 mm (maximum 9.6 mm), depths averaging 2-3 mm (maximum 5.1 mm);

subtriangulate hinge line in ventral beak area; minute ventral beak overhanging hinge; small anacline area; transapical foramen displaying small, protruding pedicle collar; anterior commissure rectimarginate; outer primary shell layer, in well-preserved shells, showing concentric laminations, slightly raised ridges with radial fibres. Internally, shell wall thick; pedicle cavity infilled with thick callist surrounding pedicle collar, with collar base fused to callist; teeth short, thick, stumpy, without lateral lobes; dorsal hinge plate thick, massive; narrow, short cardinal pit expanding to V-shaped groove distally, bifurcating into notches flanking high median septum; socket plates forming thin lining to sockets; crural bases minute, pointed apically, terminating in divergent, gently arched, feathery crura; jugum gently arched, ending medially in small jugal plates(?); spiralia dorsally directed, with ca. 3 whorls.

Remarks. In serial sections this species shows dorsally directed spiralia, thick walls, pedicle callist and collar, and teeth, hinge plates of *Lissatrypa*. The external fibrous or villose ornament is highly variably developed with some specimens almost entirely covered, and others lacking this. Most of the Whittard specimens examined were ground down (possibly by Whittard) on the dorsal side to display spiralia; this left fewer whole shells available for selection of types or serial sections. The species is distinguishable from *Lissatrypa obovata* (Sowerby, 1839), in being nearly half the size, and in possessing a more triangulate, straight-edged hinge (*obovata* being nearly perfectly round). In simplified sections Rybnikova (1967, fig. 33) illustrated the apex and hinge plate of a Latvian species *L. minuta*, demonstrating similarity to those of British *Lissatrypa*, although no pedicle callist or collar, spiralia nor jugal processes, were shown

Fig. 75. *Lissatrypa* cf. *minuta* (Rybnikova, 1967). Statistical comparison [see *L. obovata*] for specimens from the type locality [closed circles], and from Devil's Dingle locality, Telychian, late Llandovery [open circles].

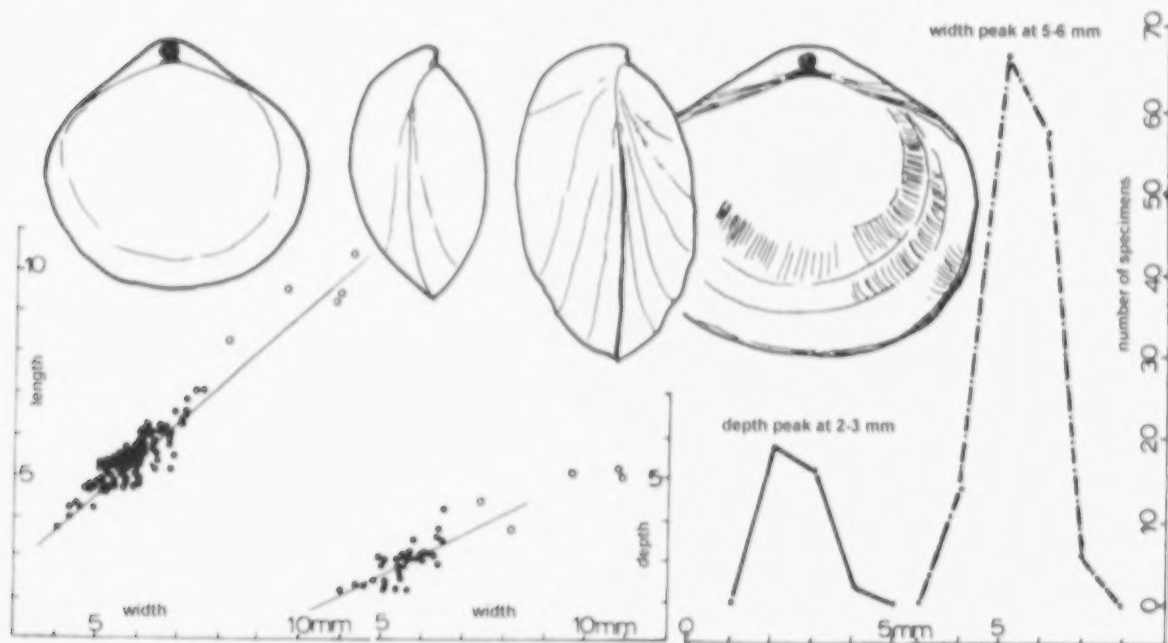
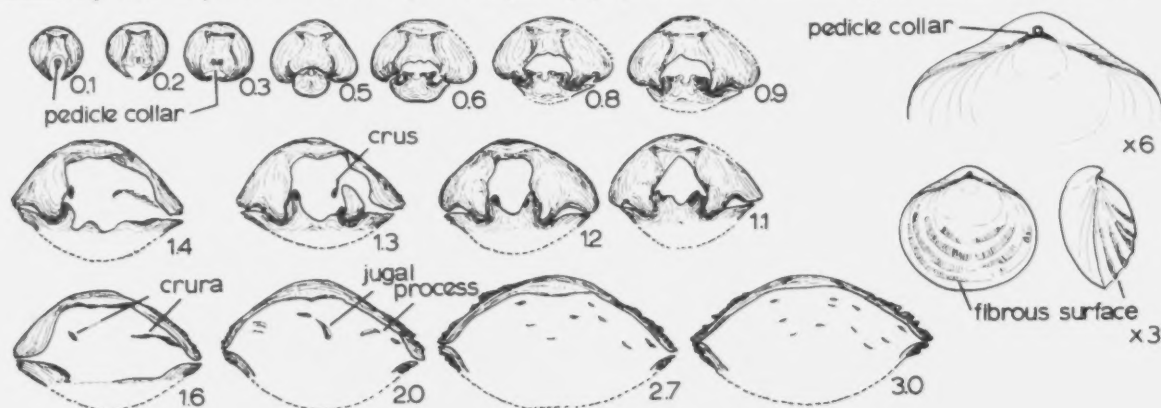


Fig. 76. *Lissatrypa* cf. *minuta* (Rybnikova, 1967). Serial sections of partly polished specimen from Loc. 134, Harley Brook, Telychian, late Llandovery. Note the pedicle callist, offset spiralia, displaced jugal processes. $\times 5$. Sketch of typical external views, ca. $\times 10$.



[these are small, and may have been missed]. The Latvian specimens ranged from 7 to 9 mm in width, only slightly larger (2–3 mm) than the British material, and their similar shape also suggest they are conspecific. *Lissatrypa minuta* Kulkov 1967a, from Wenlock strata of the Altai mountains, reaches widths up to 8.5 mm and has a weak anterior fold [there is also no data available on its spiralia and jugal processes]. *Glassia minuta* Fu 1982 is also a slightly larger, but similarly shaped, species. The new species *L. minuta* described by Doyle, Harper, and Parkes (1990) fits into the diagnosis of Rybnikova's species of *minuta*. Since the Latvian, Siberian, Irish, and Chinese specimens all carry the same species name, the older Rybnikova name remains valid.

Materials. Total 171 specimens [Whittard collection], mostly from the Hughley Shale, Telychian (C5?), late Llandovery. The species is unknown in the Lower Visby beds on Gotland. Locality, **Harley Brook**, locality 134, S bank Harley Brook, 270 yards SW Domas, 5J 5936:0062, BC11274-9, BC11283-5 [167: unfortunately most of the specimens in this collection, misidentified as *Glassia*, have had the dv ground down, thus obliterating many structures]; **Devil's Dingle**, temporary exposure for dam near Buildwas, locality R5, BC11286-7 [4: these specimens range to 12 mm in width, and may be a different species]. The specimens are accompanied by shells of the catazygine *Pentlandella*, confirming its late Llandovery age.

Lissatrypa obovata (Sowerby, 1839)

Pl. 26B, figs. a–m; Figs. 77–79

- 1839 *Atrypa obovata* Sowerby, p. 618, pl. 8, figs. 8–9.
 1851 *Spondylobolus craniolearis* M'Coy, p. 408.
 1852 *Spondylobolus craniolearis*, M'Coy in Sedgwick and M'Coy, p. 255, pl. 1H, figs. 4–5.
 1867 *Athyris obovata*, Davidson, pl. 12, fig. 19.
 ?1878 *Atrypa obovata*, Haupt, p. 65–66, pl. 2, figs. 5a–c.
 1881 *Glassia obovata*, Davidson, pl. 5, figs. 1–2.
 1882 *Glassia obovata*, Davidson, pl. 7, figs. 11–20.

Type locality and stratum. 'Lower Ludlow Rock . . . Mathon Lodge, west flank of the Malvern Hills' (Sowerby, 1839). The lectotype GSM6624, chosen by Bassett and Cocks

(1974), is from Mathon Lodge, and of lower Ludlow (Gorstian) age, probably within the *nilssoni* Zone. An attempt was made to rediscover the original locality described at Mathon Lodge (a hotel in 1990), but there are no longer any outcrops at or very near the locality, despite a search permitted and information provided by the owners. No other specimens from the Mathon Lodge, or the Malverns, were located in the British Museum, Sedgwick, and Birmingham collections. Nevertheless, Watkins (1979) found 630 specimens of '*Glassia*' *obovata* from the middle Elton beds nearby at Perton, Millichope, and Ledbury. The specimens in museum collections most commonly are labeled as 'Dudley', probably from the 'Upper Quarried Limestone' of late Wenlock age, or slightly above in the lower Elton beds. However, the Dudley stratigraphic collecting horizon remains uncertain, as it includes beds from the high *lundgreni* through *ludensis* zones (Ratliffe and Thomas, 1999). The Dudley specimens appear to be morphologically identical to the original figures, except in being slightly larger than the Sowerby lectotype from Mathon Lodge, which was examined. The type locality suggests that the specimens were derived from an outer or distal ramp or shelf facies, in somewhat deeper waters. However, the Dudley specimens came from a more proximal shelf facies in the Midlands. Davidson (1882, p. 118) stated he had access to specimens from the Wenlock Shales in a railway cutting near Dudley, and also had specimens from the 'Wenlock Shales of Woolhope', which he illustrated on pl. 7 (figs. 11–20; as 'Wenlock Shale, Shropshire').

Diagnosis. Rounded, biconvex *Lissatrypa*, averaging 10–11 mm wide, 5–6 mm deep, rectimarginate to very weakly plicate commissure; internally pedicle collar present; teeth short, stubby; dorsally directed spiralia with up to 6 whorls.

Description. Medium sized, biconvex; 10–11 mm wide (average 10 mm), slightly wider than long, 5–6 mm deep (average 5 mm); round outline; beak rounded, blunt; vv umbo incurved; area anacline–hypercline; foramen transapical, round, with centred small pedicle collar; hinge angle 120°–130°, averaging 122°; hinge line rounded at corners, no medial indentation; anterior commissure usually rectimarginate, especially in early stages of growth, rarely weakly folded;

Fig. 77. *Lissatrypa obovata* (Sowerby, 1839). Statistical variation compiled for specimens from the Much Wenlock Limestone, 'Dudley', late Wenlock; camera lucida sketch of typical specimen.

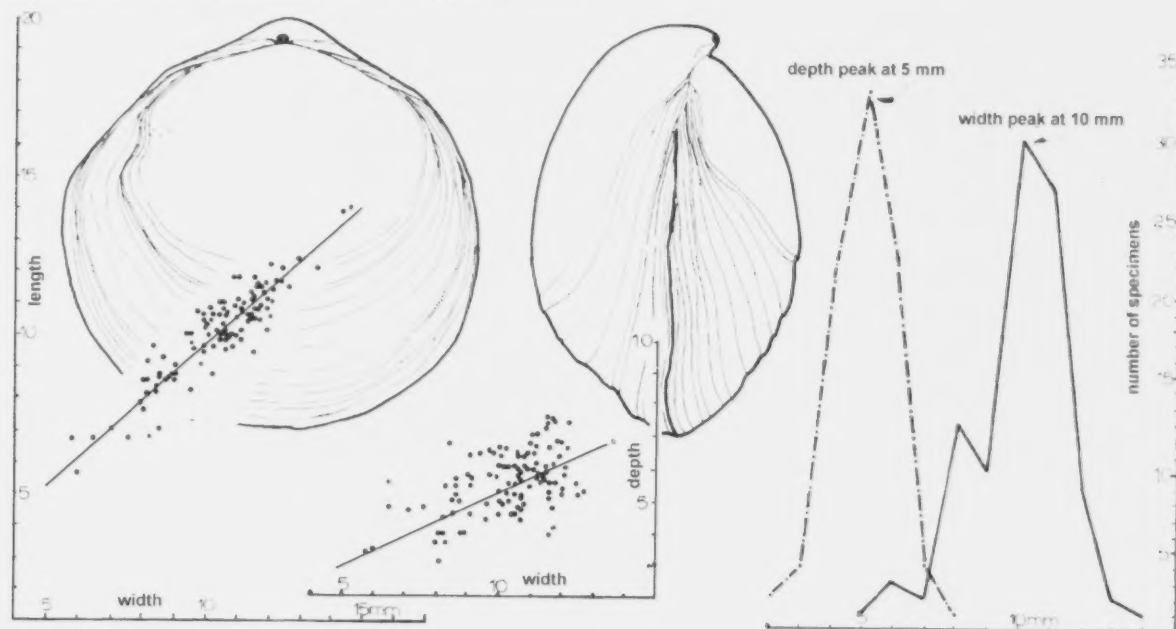
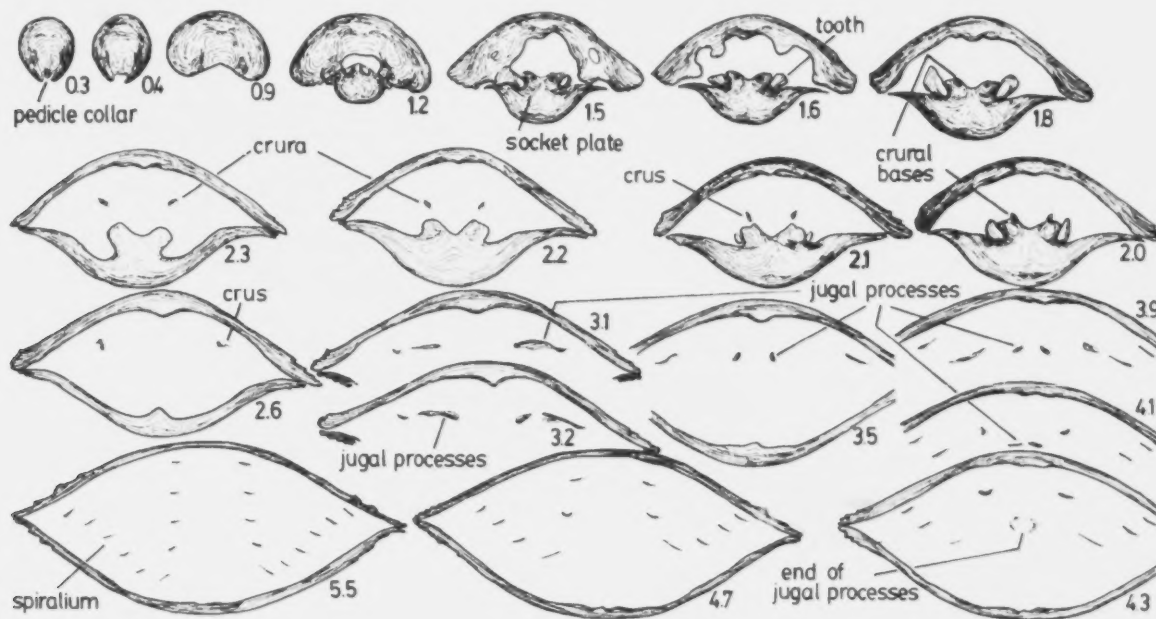


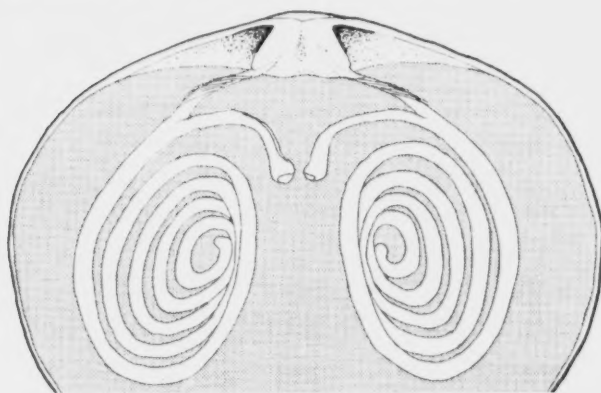
Fig. 78. *Lissatrypa obovata* (Sowerby, 1839). Serial sections of hypotype A24691, 'Dudley', late Wenlock; note thick pedicle callist, deeply indented muscle scars, $\times 5$.



surface normally completely smooth, but for overlapping growth interruptions at commissure rarely fibrous or villose. Internally, thick shelled; wide pedicle callist spanning space posterior to teeth, leading to small collar; diductor scars strongly incised, small, one fourth to one fifth shell length, variable in shape from rounded to reniform, separated by somewhat high septum, with small fused adductor scar

postero-medially; cardinal process absent; ventral adductor scars reaching one third to one half shell length, lobed in three sections; teeth very short, blunt, lacking lateral processes; anterior crural notch; massive, thick, raised hinge plate, rather flat in centre; short, narrow, blunt socket plates; bulky inner socket ridges; large, rounded crural bases; minute crura; jugal processes short, weakly curved, ending

Fig. 79. *Lissatrypa obovata* (Sowerby, 1839). Reconstruction of A24691, 'Dudley', late Wenlock; see Fig. 78, $\times 6$.



curved sharply nearly 360° ; minute sickle-shaped jugal plates forming rounded tube or ring in plane of symmetry; spiralia fewer than 6–7 whorls, dorsally directed with apices near plane of symmetry.

Remarks. *Atrypa obovata* (Sowerby, 1839) was initially selected as the type species of the genus *Glassia* by Davidson in 1881. Unfortunately, Davidson used specimens of another species he named at the same time, *Glassia elongata*, to demonstrate and characterize the highly distinctive, medially directed spiralia (prepared by Maw), not realizing that the smooth atrypoid *obovata* of Sowerby was internally very different (Copper, 1996b). He probably thought that all smooth shells were the same inside, as did others much later. Specimens of '*Atrypa*' *obovata* from the Much Wenlock Limestone have been sectioned, and reveal that the species has dorsally directed spiralia and a hinge plate identical to those belonging to the type species of the genus *Lissatrypa* established by Twenhofel in 1914. *Lissatrypa* also has a thick shell, solid teeth lacking dental plates, pedicle callist commonly leading to a collar, and jugal plates ending in a rounded configuration. This is quite unlike anything seen in the Glassiinae, e.g., *Glassia elongata* and *G. djavvika*. Taxonomically, therefore, *Lissatrypa* is a junior synonym of *Glassia*, as the type species are internally the same. The Glassiidae, as defined by Schuchert and Levene (1928) for those taxa with medially directed spiralia, and the Lissatrypidae Twenhofel (1914), originally defined with dorsally directed spiralia, would need to be conceptually reformed. The name *Lissatrypa* would have to be suppressed, and an alternate genus selected for those smooth atrypids with medially directed spiralia, and a new family name erected for those with medially directed spiralia. To avoid this nomenclatorial nightmare, to maintain taxonomic stability, to prevent the proliferation of new names, and to conserve evolutionary sense, the most rationale approach has been to redesignate the other alternate Davidson species for *Glassia*, *G. elongata* 1881. As the type for *Glassia*, it has medially directed spiralia described originally by Davidson to define the genus. In addition, the species *obovata* is thus re-assigned to the genus *Lissatrypa* (vide Copper, 1996b, 2001c).

Part of the confusion in differentiating '*Glassia*' *obovata* and *Glassia elongata* stems from the misinterpretation of

specimens of *obovata* for which Maw (Davidson's assistant) removed part of the dorsal shell wall of '*Glassia obovata*' to show the spiralia (Davidson, 1881, pl. 7, figs. 17–18; specimen B5498). Since the spiralia point dorsally with their apices almost meeting in the shell centre, such prepared *Lissatrypa* specimens show apparent, but not genuine medial direction of the spiralia [refer to *Glassia elongata* for the shell structure, and direction of medially oriented spiralia]. This is clarified with serial sectioning only. Although *Lissatrypa* is absent in Gotland outcrops today, a German glacial erratic specimen labeled '*ovata*' by Haupt (1878, pl. 2, fig. 5) suggests it may occur in Pridoli strata below sea level south of the island.

Materials. Total 78 specimens; none available from the type locality in the Malverns. **Dudley**, Wenlock Limestone, A26456–70 [15], A26477–91 [13], B5499 [6], B5498 [1], B619 [4], B8619 [7], B23221 [4], B24281 [6], B5497 [15: the collections here were said to be mixed with those from 'Ledbury']; **'Dudley'**, Wenlock Shale, A26471–6 [5]; **'Dudley railway cutting'**, Wenlock Limestone, B23042 [2]. The species may range up into higher Ludlow strata in Britain where it has been commonly reported (e.g., Watkins, 1979). The species appears unknown from 'Wenlock Edge' collections.

Lissatrypa compressa (Sowerby, 1839)

Pl. 26C, figs. a–e

1839 *Atrypa compressa* Sowerby, p. 629, pl. 13, fig. 5 [see holotype, plate 26C, figs. a–e].

1867 *Athyris compressa*, Davidson, p. 122–123, pl. 12, figs. 16–18.

Non 1879 *Atrypa compressa*, Barrande, 1879, pl. 85, figs. 1, 1–10 [= athyridid with lateral spiralia].

?1982 *Glassia compressa*, Cocks and Baarli, pl. 2, figs. 1–5.

Type locality and stratum. 'Wenlock Shale. Woodside and Nash near Presteigne' (Sowerby, 1839). Cocks (1978) determined that the lectotype came from shales of Wenlock age near Woodside, Presteigne, which becomes the general type locality: the precise locality and level are unknown, and no new data is available. Wenlock shales here span the *rigidus* to *ellesae* zones, and are of middle Wenlock age (Sheinwoodian). Davidson (1867) believed that the type specimen of *compressa* came from the Woolhope Limestone (in the Geological Survey collections Davidson labeled this as the Woolhope beds), but this cannot be confirmed, as no other collections from this level appear to exist. The Woolhope Limestone is within the lowermost Wenlock, *centrifugus-murchisoni* zones, i.e., below the Wenlock Shale, so the type specimens could be of early Sheinwoodian age. Cocks (1978) identified the holotype, by monotypy, from the Sowerby collections as GSM6625 [see Fig. 123]. The Malverns location suggests a mid- to distal shelf (almost at the shelf edge near Wenlock Edge), or a carbonate ramp setting, in deeper waters.

Remarks. Davidson (1882) remarked that 'after a very careful study of all this material it appeared to me that the so-called *Atrypa obovata* and *A. compressa*, of Sowerby, are nothing more than modifications in shape of a single species'. Davidson may have been correct. *Lissatrypa* species

are notoriously difficult to separate, as nearly all fit more or less into the same 'mould', varying externally only somewhat in size, globosity, hinge line, and commissure. This species remains enigmatic, as no new materials were discovered in collections from the type locality or region. The anterior sulcation of the vv, seen in the type and only definitive specimen, could be an artefact of preservation, or slight compression. Until fresh new collections reveal clear differences, this species remains in doubt. Specimens from the Buildwas localities appear to be somewhat more similar to the figured type in having a low fold on the anterior commissure, generally missing on *L. obovata*. These are thus listed under the name *L. compressa*. The lack of good material for sectioning prevented further description. The smooth brachiopod '*Rhynchonella*' *callawayiana* (Davidson, 1883, pl. 10, figs. 30a-c) from the Coalbrookdale Fm. (= Wenlock Shale) of Walsall, with its high anterior fold, is probably a variety of *Septatrypa* [the type specimen is lost, Cocks, 1978, p. 159].

Materials. Total 42 specimens examined, but these shells are not significantly different from *L. obovata*, except in the weak anterior fold. Type locality, **Woodside**, Presteigne, GSC6625 [1]; **Buildwas**, 'Wenlock Shale' A27294-8 [5], B5500-1 [2], B24120 [3], B34854 [25]. The exact horizon of the latter locality is also not known, but these shells probably are from the Buildwas beds, of early Wenlock age. **Lincoln Hill** [6], collected from *Plectatrypa marginalis* and *Atrypa harknessi*-bearing beds [Wenlock Shale] at a temporary excavation for a house at Lincoln Hill.

Atrypoides Mitchell and Dun, 1920

[= *Atrypella* Kozłowski, 1929; = *Globatrypa* Mizens and Sapelnikov, 1985; = *Lingatrypa* Mizens, 1985]

Type species. *Meristina* (?), sic) *australis* Dun 1904, New South Wales, eastern Australia, Ludlow.

Range and distribution. Aeronian, South China(?); Wenlock-Pridoli, worldwide, except Malvinokaffric province. Doubtful, occurrence in early Lochkovian, Czech Republic (Havlíček, 1987a).

Diagnosis (as in Copper, 1977b, with following emendations). Early growth stages, and possibly early species in the evolution of the genus, may have a small orthocline area with an apical foramen flanked by small deltidial plates. Pedicle callist absent; dorsal septum absent or weak.

Remarks. The origin of the genus is still obscure. Some early workers (Siemiradzki, 1906a, b) regarded simple convexity as sufficient to assign Dalman's species *prunum* to the ribbed Devonian, biconvex genus *Gruenewaldtia*. Sapelnikov and Mizens (1982) regarded *Atrypoides subrecta* (Mizens, 1977), from probable (?) late Llandovery rocks of the central Urals, as the ancestral species. Wang et al. (1980) found evidence of Aeronian and earliest Wenlock *Atrypoides* in China, so the genus may have originated there before migrating widely in the Ludlow. The earliest Gotland species, early Ludlow *A. sulcata* (Lindström, 1861) is a smaller biconvex *Atrypoides* with an orthocline area and apical foramen flanked by distinctive deltidial plates in its neanic stages. *Atrypoides* is absent in Britain.

Three species of *Atrypoides* are known on Gotland, one of these new, and all of these occur within the central to eastern, marginal onshore shelf, biostromal settings, and, less commonly, reefal facies of the Hemse beds. *Atrypoides* is abundant to common at only a few localities on Gotland, e.g., the type localities of *A. sulcata*, the earliest species, and *A. prunum*, a later species, on the east coast. *A. hemsea* n. sp. is confined to reefal and peri-reefal localities of the interior of Gotland: it is only slightly younger in age than *A. prunum*. The stratigraphic range of *Atrypoides prunum* is said to be considerably greater in the eastern Baltic (Estonia; Kaljo and Rubel, 1982); however, that may contain the species *A. saaremaensis* (Copper and Rubel, 1977) from the latest Ludfordian, absent on Gotland. The genus is absent in Britain, a feature related to lack of appropriate facies and environment, i.e., very shallow, nearshore back-reef or lagoonal carbonates. *Atrypoides* is not known from Wenlock age rocks in Gotland and Estonia, suggesting that it is an eastern immigrant from the Urals, Siberia, or South China. In Arctic Canada *Atrypoides* is also only known in rocks of Late Silurian age (Ludlow-Pridoli; Jones, 1981). However, in the Hudson Bay Lowlands *Atrypoides* is reported as early as the late Llandovery (Jin et al., 1993), suggesting a migration pathway westwards, bypassing Baltica.

Atrypoides is a major element in many Late Silurian marine carbonate shelf communities around the world, often dominating the local benthos and forming an *Atrypoides* community (Kaljo and Rubel, 1982; Jones, 1982). This speaks for its evolutionary success at this time in shallow, proximal settings on carbonate platforms. It may also account for the large number of species or varieties assigned to it. The significance of all these species is not clear. Mizens and Sapelnikov (1982) drew an evolutionary diagram of the species known in the Urals region, suggesting that the ancestor of the whole genus complex was *Atrypoides subrecta* from the late Llandovery, and that three co-existing stocks (species clusters or lineages) existed in Wenlock, Ludlow, and Pridoli times. These three stocks were later identified as *Atrypoides* s.s., *Globatrypa*, and *Lingatrypa*, on the basis of convexity and variation in the dorsal fold. The only apparent character to differentiate these is their external shape, *Globatrypa* being more globose and *Lingatrypa* being flatter: internally no structural difference is evident. Herein I have arbitrarily lumped these three species-groups, although the reef-dweller, *A. hemsea*, with a broad anterior fold, could be aligned with *Lingatrypa*. Modzalevskaya and Nikiforova (1982) regarded *Atrypoides* and *Atrypella* as distinct genera, but the rationale for this is not evident, as there is no internal difference (Copper, 1977b). Jones (1974-1983; Jones and Packard, 1980; Jones and Rong, 1982; Jones and Narbonne, 1984) have made the most serious attempt to date to determine the statistical validity of at least the Canadian Arctic and Chinese species. Jones (1979b) came to the conclusion that the primary controls to external morphology were basinal or regional environmental variation, not evolutionary, and this assessment is probably correct. On Gotland, the occurrence and broad, flat fold of *A. hemsea* suggests that this species, like *A. bioherma* (Jones and Narbonne, 1984), was adapted to reef habitats. However, the Arctic species occurs in deeper water reefs between below wave base to storm base: the Gotland species belongs to a very shallow water

reef setting only a few metres deep (Watkins, 1975: described this Gotland species as *Lissatrypa*). This suggests that *Atrypodea* on Gotland was selective as to substrate habitat, or subject to strong competition from other fauna, moving into an area only when conditions were appropriate. This setting was primarily very shallow, relatively quiet water, lagoonal or back reef.

Species assigned [in addition to the 38 species or subspecies cited in Copper, 1977b]. The genus appears to reach a diversity peak in the Pridoli (based on species described), but maximal abundance was in the Ludlow. Devonian records are suspect (Smith and Johnson, 1977). Havlíček (1999) recorded an '*Atrypodea* sp. A' from the Lochkovian of the Prague Basin, on the basis of rare, incomplete specimens that were not examined internally. More than 42 species or subspecies are described from the Urals, and 13 spp. from China. The following additional 56 species have come to light, bringing the total to 93 *Atrypodea* species, subspecies, or varieties, which is remarkable for a smooth shell with so few diagnostic external characters. Nine species are recorded from the Prague Basin. In total, this is probably a record for atrypoids in general. In the Urals, various attempts have been made to zone the Ludlow–Pridoli section using *Atrypodea* species and varieties, with some success (e.g., Modzalevskaya 1968, 1980, 1981; Mizens, 1977, 1981, 1985; Beznosova, 1977, 1994; Beznosova and Mizens, 1980; Modzalevskaya and Nikiforova, 1982).

Atrypodea bailongjiangensis Fu 1982, Bailongjian, Qinling Mountains, China, Yanglugou Fm., Pridoli.

Atrypodea bioherma Jones and Narbonne 1984, Somerset Island, Arctic Canada, Douro Fm., middle Ludlow.

Terebratulina camelina Buch 1840, 'Bogoslovsk', E slopes central Urals, Pridoli (see Sapelnikov and Mizens, 1991).

?*Atrypa cephe* Barrande 1879, Konieprus, Prague Basin, étage F2, ?Pragian [very doubtful age assignment].

?*Atrypa linguata* var. *columbella* Barrande 1879, Lodenitz, Prague Basin, étage E, Lochkovian [doubtful].

Lissatrypa cuboidiformis Khodalevich 1938, Losva River, Urals, upper *marginalis* Horizon, ?Pridoli.

Terebratulina linguata var. *columbella* Barrande 1847, Prague Basin, Lodenice–Luzce, Pridoli.

Atrypella scheii forma *crassa* Modzalevskaya 1981, Chernyshev Range, Prepolar Urals, Pridolian.

?*Meifodia discoidalis* Jin, Caldwell, and Norford 1993, Attawaspiskat River, Hudson Bay Lowlands, Telychian [possible early *Atrypodea*, and probably = *A. praelingulata* Jin et al., 1993].

Atrypodea dorsocomvexa Wang, Rong, and Yang 1980, Qujing, Yunnan, Kuanti Fm., Ludlow [= ?*foxi* Jones, 1974: see Jones and Rong, 1982].

Atrypodea elatior Havlíček 1991, Stydlé vody Hill, Prague Basin, upper Pridoli Fm., late Pridoli [possibly youngest known species].

Atrypodea erebus Jones 1979a, Prince Leopold Island, Arctic Canada, Leopold Fm., early Pridoli.

Lissatrypa penitus elongata Khodalevich 1939, Isov region, Urals, Striatov beds, Ludlow.

Atrypodea scheii forma *fossula* Beznosova and Mizens 1980, Foma-Yu River, Urals, Greben Horizon, Pridoli.

?*Atrypa fugitiva* Barrande 1879, Kolednik, Prague Basin, Lochkovian [probably athyridid *Anoplothea*].

Atrypodea gashaomiaensis Su, Rong, and Li 1985, Gashaomia, Inner Mongolia, Xibiche Fm., Ludlow.

Lissatrypa gigas Khodalevich 1939, Sosva River Basin, N Urals, Bobrov Horizon, Pridoli.

Atrypodea gigantus Jones 1981, Goose Fiord, Ellesmere Island, ?early Pridoli.

Atrypella insigne var. *grebensis* Nikiforova 1970, Ufim, Urals, Karpov Horizon, Pridoli.

Atrypodea hemsea n. sp., Gotland, upper reefal Hemse beds, Ludlow.

Atrypella inflata Fang 1974, Qujing, Yunnan, Miaogao Fm., late Ludlow – ?early Pridoli (see Rong and Yang, 1980; Fang et al., 1985).

Atrypodea jiudishanensis Tong 1984, Jiudishan, Sichuan, Jiudishan Fm., Ludlow.

Atrypella camelina karpovensis Nikiforova 1970, Vaigach Island, Greben beds, N Urals, Pridoli.

Atrypodea elongata lata Sapelnikov and Mizens 1982, Vargan River, N Urals, Pridoli.

Atrypodea ladzeica Beznosova 1977, Pai-Khoi, N Urals, Pridoli.

Protathyris lentiformis Wang 1956b, Chinguishan, Yunnan, South China, Xiushan Fm., Wenlock–?Ludlow [see Wang et al., 1980].

Terebratulina linguata Buch 1835, p. 101, 'Kalkstein der Gegend von Prag', [sensu Barrande 1847, pl. 15, figs. 2a–c: see Havlíček, 1990], Dlouha Hora, Beroun, Prague Basin, lower Kopanina Fm., early Ludlow [= type of *Lingatrypa*].

Lissatrypa linguifera Khodalevich 1939, N Urals, Vagran River, Ludlow.

Atrypella phoca forma *longa* Nikiforova, 1970, Vaigach, N Urals, Ludlow (see also Modzalevskaya, 1980).

Glassia obovata var. *magna* Grabau 1925, Yichangdazhongba, Hubei, Luoreping Formation, Ludlow–Pridoli [see Wang et al., 1964, p. 434].

Atrypodea minzhini Rozman 1988 [identified as *Atrypella* in figures, *Atrypodea* in text], Gobi Altai, Mongolia, upper Tsaganbulak beds, early Ludlow.

Atrypodea polaris modica Rong, Zhang, and Chen 1987, Qinling Mountains, China, Yanglugou Formation, Pridoli.

Lissatrypa nasa Nikiforova 1949, Arg River, Gissarsk Mtns., Kirgizstan, Marginalev beds, Ludlow.

Atrypella neimongolica Hou and Zhao 1976b, Daerhanmaominan, Lianheqi, Inner Mongolia, Late Silurian.

Atrypodea netserki Jones 1981, Beechey Island, Arctic Canada, Barlow Inlet Fm., early Pridoli.

Atrypodea ohsa Fang 1985, Qujing, Yunnan, Yuejiashan Fm., Wenlock.

Lissatrypa operosa Kulkov 1967a, Chergi River, central Altai, Kuimov Suite, Ludlow.

Atrypella camelina pavdensis Mizens 1977, E slopes N and central Urals, Elva River, Wenlock.

Lissatrypa penitus Khodalevich 1939, Urals, lower Striatov beds, Ludlow.

Atrypodea pentagonalis Beznosova and Mizens 1980, Bolshaya Sinya River, Urals, Greben Horizon, Pridoli.

- Atrypoides planata* Perry 1984, Yukon, Canada, 193–204 m above base of Delorme Fm., Ludlow.
- Atrypoides polaris* Jones and Packard 1980, Cornwallis Island, Arctic Canada, Mbr. C, Read Bay Fm., late Pridoli.
- Atrypoides praelingulata* Jin, Caldwell, and Norford, 1993, Hudson Bay Lowlands, Severn River, Telychian [see *Meifodia discoidalis* above].
- Atrypoides quadrata* Fu 1982, Qinling Mountains, China, Ludlow–Pridoli.
- Atrypoides quijiangensis* Wang, Rong, and Yang 1980, Qujiang, Yunnan, Kuantu Fm., Ludlow [= *foxi*: see Jones and Rong 1982].
- Terebratulina renitens* Barrande 1879, Zadni Kopanina, Prague Basin, lower Kopanina Fm., early Ludlow.
- A. saaremaaensis* Copper and Rubel 1977, Saaremaa Island, Estonia, Kuressaare beds, late Ludlow.
- Atrypella scheii concinna* Oradovskaya 1975, Kolyma River Basin, Omulev Mountains, Bison Horizon, Late Silurian.
- Lissatrypa sphaerica* Sapelnikov 1956, Altai Mountains, Ludlow.
- Atrypella subrecta* Mizens 1977, Semenov village, E slopes N and central Urals, Wenlock.
- Atrypella scheii forma superba* Modzalevskaya 1981, Chernyshev Range, Prepolar Urals, Pridolian.
- Atrypoides tianshanensis* Rong and Zhang, 2001, Heiyingshan, Xinjiang, Yiqikebash Fm., Ludlow–Pridoli.
- Atrypoides trapezoida* Fu 1983, Qinling Mountains, China, Ludlow–Pridoli.
- ?*Lissatrypa turjensis* Khodalevich 1939, Isov region, Urals, Elkin Horizon, Wenlock.
- Lissatrypa uralica* Khodalevich 1939, Yatrín River, N Urals, Striatov Horizon, Ludlow.
- Lissatrypa vagranica* Khodalevich 1939, Nadezhda region, Urals, *marginalis* beds, Ludlow.
- Atrypoides vangyrice* Beznosova and Mizens 1980, Chernysheva, Vangyr River, Urals, Greben Horizon, Pridoli.
- Atrypoides ventriplanata* Wang, Rong, and Yang 1980, South China, Ludlow.

Note: Sapelnikov and Mizens (1982) removed *Atrypa kuschensis* Chernyshev 1893 from *Atrypoides*, and placed it in the genus *Lissatrypa*, distinguishing it from *Atrypoides*, and citing other species as synonyms or as subspecies. Mizens and Sapelnikov (1985) erected *Globatrypa*, type *Merista globus* Chernyshev 1885, previously identified by Copper (1977b, p. 15) as an *Atrypoides*, as a separate species-group on the basis of its more rounded and globose shape. *Globatrypa* is herein regarded as a morphologic variant of *Atrypoides*, as it is internally identical and grades externally into other *Atrypoides* variants, including the globose type species of *Atrypoides*. *Lingatrypa* Mizens 1985, type *Terebratulina linguata* Buch 1835, has a relatively flatter vv, broad anterior fold, and small deltidial plates. This is a reef-inhabiting variant of *Atrypoides*, like *Atrypoides planata* Perry 1984 and *A. bioherma* Jones and Narbonne 1984 (see also *Atrypoides hemsea* herein), and is here also not regarded as a clearly distinguishable subgenus.

Jones and Rong (1982) placed three previously listed species in synonymy (see above). Jones (1982) and Jones and

Narbonne (1984) stated that Canadian species of *Atrypoides* were ecologic variants and thus of limited biostratigraphic value. This is probably just, as no distinct shape trends are evident, although late Ludlow and Pridoli varieties may be the largest. Nevertheless, they cited a stratigraphic sequence of *Atrypoides phoca-foxi-erebus* in the Canadian Arctic, thus postulating an evolutionary trend. The three *Atrypoides* species from Gotland show no clear morphological trends with time. The earliest species *A. sulcata* (early Ludlow, early Gorstian, *nilssoni* Zone) is quite small, *A. primum* is the largest (*tumescens* Zone, late Gorstian), and the youngest, *A. hemsea* (high *tumescens-leintwardinensis* zones, early Ludfordian), is medium to large sized. The youngest in the Baltic Basin, *A. saaremaaensis* from Estonia (*formosus* Zone, late Ludfordian), is even larger than *A. primum*.

Atrypoides sulcata (Lindström, 1861)

Pl. 27A, figs. a–q; Figs. 80–82

- 1861 *Spirigerina sulcata* Lindström, p. 364, pl. 12, figs. 4 (4 views).
- 1890 *Atrypa phoca* Salter, Gagel, pl. 1, figs. 32a–b ['Ragnit', glacial erratics, N Germany].
- 1974 *Lissatrypa ?sulcata*, Bassett and Cocks, pl. 9, figs. 1a–d.

Type locality and stratum. 'Stranden af Kräklingbo vid Hammarudd' (Lindström, 1861, p. 355). The locality name 'Hammarudd' appears on modern maps as a point along the coast, but this species is absent there. The Lindström collection was available for study. Abundant specimens of *Atrypoides sulcata* occur in only two readily accessible sites on the NE coast today, namely at Garnudden 5 and 9, in the bay between Hammarudden and Garnudden, about 700 m NW of the former. Garnudden 5 is probably the same one sampled by Lindström (and known to Schmidt in 1859; material also occurs in the Hisinger collection). Specimens in Lindström's collection are identical to new material found, and shells are most abundant there. The type locality 'Hammarudd' in old collections [= Garnudden 5, locus typicus restrictus] today consists of a 0.5 m thick outcrop of soft-weathering calcareous shales and micrites (a beach locality about 600 m S of Garnudden, east coast Gotland). It is accessible and richly fossiliferous, yielding about 85% *Atrypoides sulcata*, with the remaining shells consisting of the rhynchonellid *Rhytidorhachis diodonta* (Dalman, 1828; see Jin and Caldwell, 1990), and rare athyrids, e.g., *Didymothyris* cf. *didyma* (Dalman, 1828). This locality is designated the locus typicus restrictus. This level of the Hemse beds is the upper part of unit 'A' of Hede (1960) on the northeast coast, but stratigraphically above the *Atrypa murchisoni* level on the SW coast at Petesvik. It was said to be typified by the bivalve *Megalomus* and *Balteurypterus fischeri* (Munthe, Hede, and Lundqvist, 1929), although I have seen *Megalomus* more abundantly at slightly higher stratigraphic levels. At a second locality 200 m to the south (Garnudden 9), *A. sulcata* is directly associated with abundant large, bulbous, spherical stromatoporoids in growth position, with *Atrypoides* sometimes located in the crevices of the probable host sponge (Copper, 1977b, p. 16). This locality was known to Schmidt (1859, p. 48), who first discovered it, 'an der Spitze Ham-

Fig. 80. *Atrypoides sulcata* (Lindström, 1861). Statistical variation shown in scatter diagrams, specimens from Garnudden 5, lower Hemse beds, early Ludlow; all collected on single bedding plane over ca. 10 m²; width peak at 11–14 mm, depth peak at 8 mm; camera lucida sketches based on neanic to adult shells; N.B. deltidial plates present on neanic to medium shells, beak incurved in adult shells.

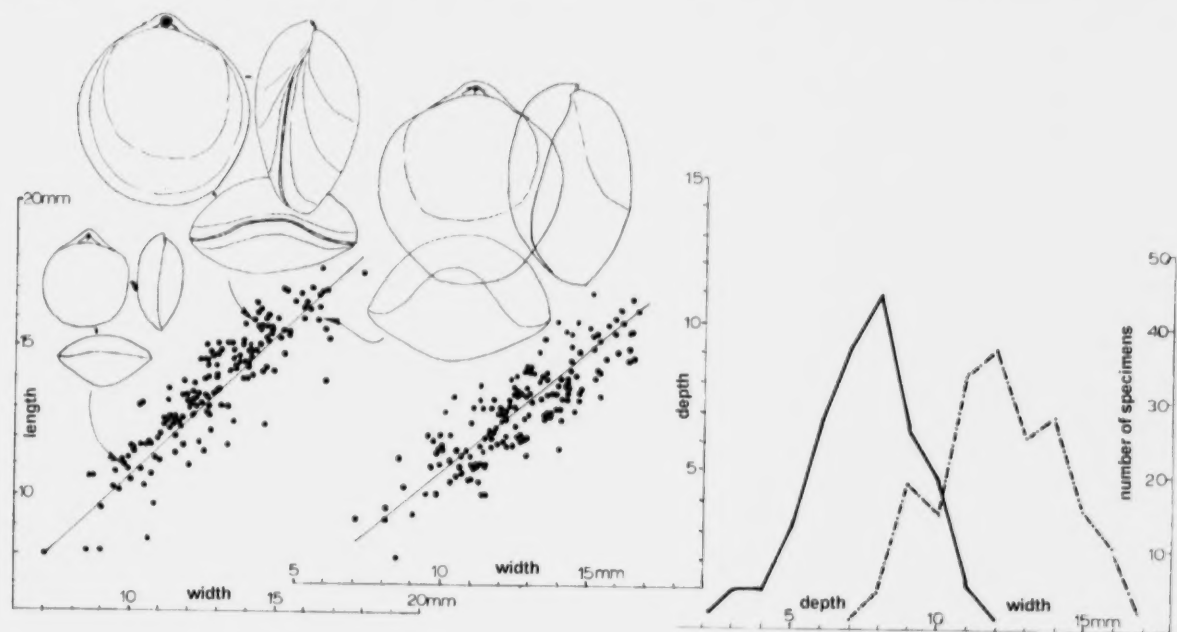


Fig. 81. *Atrypoides sulcata* (Lindström, 1861). Serial sections of hypotype Br106568, Garnudden 5, lower Hemse beds, early Ludlow; spiralia dorsally and apices slightly laterally directed; $\times 5$.

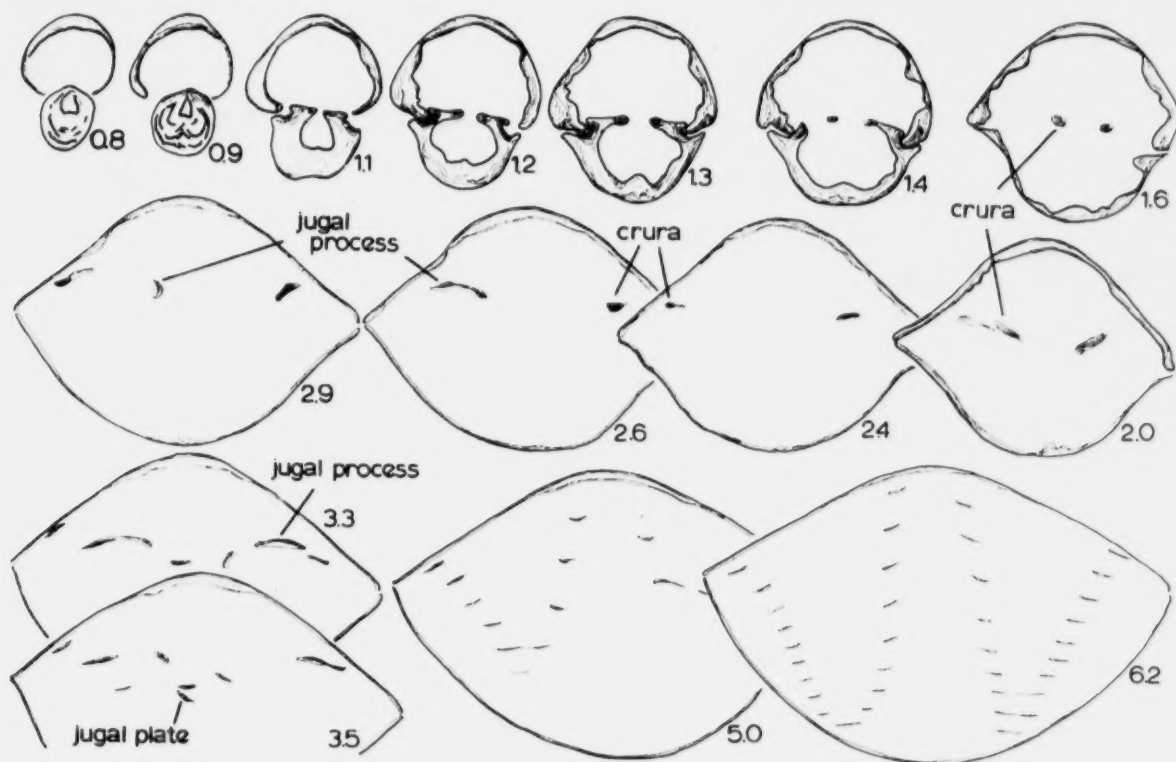
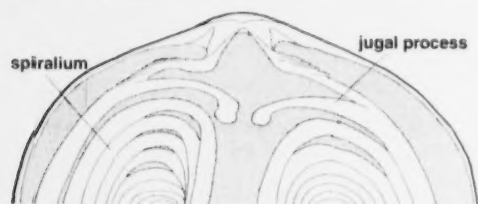


Fig. 82. *Atrypoides sulcata* (Lindström, 1861). Reconstructions from serial sections in Fig. 81, Br106568, Garnudden 5, lower Hemse beds, early Ludlow, $\times 5$.



marud selbst sahen wir einen Stromatoporen und Syringoporenkalk mit Zwischenschichten eines dunkelgrauen Mergels Garnudden 9 is estimated to be about 1–2 m above the type locality horizon. *Atrypa* is absent at both localities. The Lindström *sulcata* collection is not mentioned in mapping by Munthe, Hede, and Lundqvist (1929), who may have mistaken it for the co-occurring smooth athyridid *Didymothyris didyma*. The horizon is within the lowest ca. 5 m of the Hemse Formation in the northern facies, lower Ludlow, in the higher part of the *nilssoni* Zone. Bassett and Cocks (1974, pl. 9, figs. 1a–d) selected a lectotype for *Atrypoides sulcata* from the Hisinger collection [= Br44652], although they referred the species to *Lissatrypa*.

Diagnosis. Small to medium-sized *Atrypoides*, averaging 12 mm wide, 8 mm deep, longer than wide, with weak broad fold and commonly narrow, median groove on both valves; small deltidial plates exposed in early growth stages; transapical adult foramen.

Description. Ovoid outline, biconvex – weakly dorsibiconvex; widths from 11 to 14 mm (average 12 mm, maximum width 17 mm), lengths 12–16 mm (average 14 mm), depths 6–9 mm (average 8 mm, maximum 11 mm); maximum width at mid-shell; anterior fold broad, gently arcuate, commonly, but not always bisected by distinct groove on both valves; hinge angles 105° – 118° (average 111° – 116°); shoulder line weakly indented, shoulders rounded; lateral commissure straight; beak gently rounded; small area anacline, rarely orthocline–hypercline; foramen round, well developed, usually transapical in adults, apical in neanic stages; in neanic to medium shells, small, elongated deltidial plates developed away from foramen, generally not touching medially. Internally, shell wall relatively thick; pedicle cavity vacant, lacking callist; teeth small, directed almost horizontally into sockets, solid, lacking dental cavities and lateral lobes; narrow, elongated cardinal pit expanded into broad cavity; socket plates thin, supported by thick socket pads; inner socket ridges short, extended horizontally into plates holding rounded crural bases; curved crura partly feathered; jugal processes arched, curved in middle, directed to sides in a U-form; delicate jugal plates angled sharply to centre; spiralia dorsally directed, with 6–9 whorls; whorl lamellae thickened towards shell centre.

Remarks. This is an abundant species, marking the earliest occurrence of *Atrypoides* on Gotland (there are no Wenlock *Atrypoides* known in NW Europe). However, it appears only in a restricted set of outcrops of the lowermost Hemse beds on the east coast of Gotland, and has not been found inland, nor on the west coast. Most shells have a narrow median, or

sometimes slightly off-centre groove on both valves [hence the name *sulcata*]. Such bisulcation is also not an uncommon feature in *Septatrypa* and *Glossia*, confusing the identification of some shells. The species is less than a third the size of adult *Atrypoides prunum*, and easily distinguished from it by its less globose shape. Gagel (1890) discovered probable specimens of this species from glacial erratics at Ragnit in north Germany; these may have come from Gotland. Watkins (1975) identified '*Lissatrypa sulcata*' from reefs in the higher Hemse strata around Ljugarn; these shells are here assigned to much larger and different *Atrypoides hemsea*.

Materials. Total 312 specimens from the lowest few metres of the Hemse Formation, unit A. 'Stranden av Kråklingsbo vid Hammarudd', Lindström collection, = **Garnudden 1**, Br44597–651 [55], Br102641–646 [7]; **Garnudden 5** [SW36, restricted type locality, 182 shells]; **Garnudden 9**, 150 m S of Garnudden 5, beach locality halfway between Garnudden and Hammarudden: = ?Schmidt 1859 locality [SW37: 48 shells].

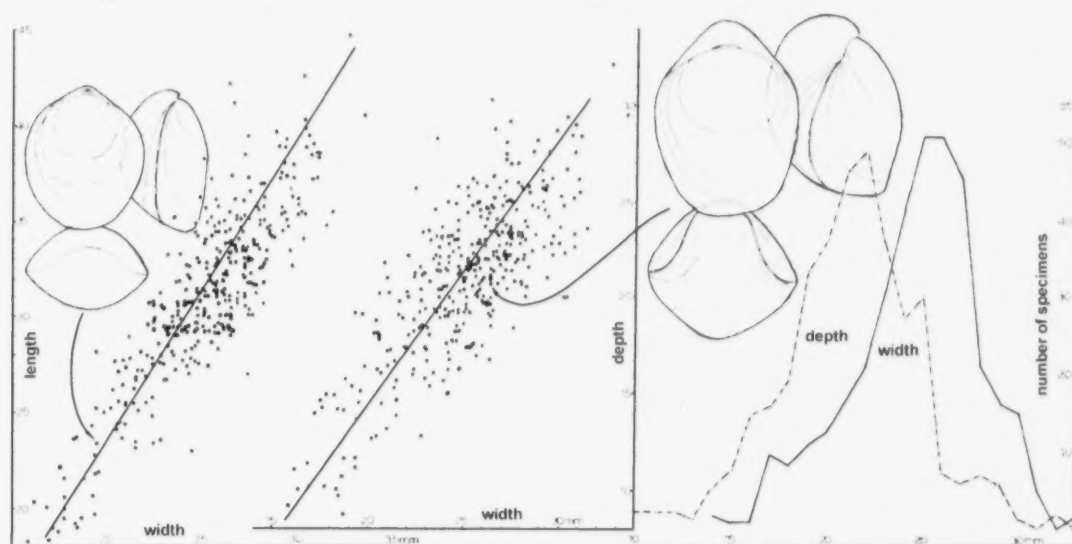
Atrypoides prunum (Dalman, 1828)

Pl. 28, figs. a–r; Fig. 83

- 1828 *Atrypa prunum* Dalman, p. 133–134, pl. 5, figs. 2a–d.
- 1828 *Atrypa prunum* Dalman, Hisinger, p. 238, pl. 5, figs. 11–12.
- 1835 *Terebratula prunum*, Buch, p. 105 [no figs., described Gotland material].
- 1846 *Terebratula prunum*, Eichwald, p. 110 [compares Gotland material with one from Orynin, Urals].
- 1860 *Atrypa prunum*, Eichwald, p. 688–689 [lumps various Ural species under Gotland *prunum*].
- 1867 *Terebratula prunum*, Quenstedt, p. 550, pl. 47, fig. 5 [specimen with first internal view of *prunum*].
- 1876 *Atrypa prunum*, Roemer, pl. 13, fig. 8 ['Insel Gotland'].
- 1890 *Atrypa prunum*, Gagel, pl. 1, fig. 36b–c ['Graudenz', glacial erratics, N Germany].
- 1924 '*Atrypa*' *prunum*, Holtehdahl, p. 129, fig. 16–6 ['Hemse group, Gotland'].
- 1970 *Atrypella prunum*, Rubel, pl. 12, figs. 1–5 [from Östergarn, Gotland].
- 1977b *Atrypoides prunum*, Copper, p. 21, figs. 3: 5–9, 4: 6–10 [Gotland material].
- 1985 *Atrypella prunum*, Nikiforova, Modzalevskaya, and Bassett, p. 40 [also Schmidt, 1875, p. 18].

Type locality and stratum. 'Gottlandia' (Dalman, 1828). The Dalman specimens were based on the Hisinger collections, which are still available, although the holotype was not specifically located (see Hisinger 1828, pl. 5, figs. 11–12: in some references the species name has been attributed to Hisinger). The horizon from which this came can be identified as the Hemse Formation, unit C: this is middle Ludlow, middle Gorstian, probably the *scanicus* Zone. If the Podolian occurrences are correctly dated, *A. prunum* occurs there also within the higher *tumescens* Zone. A rediscovered van Hoepen (1910) locality, Grogams 4, followed by Hede (1960), was initially designated as a possible type locality (Copper, 1977b, p. 21). However, a temporary south side ditch expo-

Fig. 83. *Atrypoides prunum* (Dalman, 1828). Scatter diagrams and frequency curves of specimens compiled from 'Östergarn', Gannes 4, and 'Gannes 1' collections, middle Hemse beds, Ludlow; average width peak at 25–28 mm, average depth peak at 22 mm. Camera lucida sketches of typical immature and adult shells; neanic shells not represented in data.



sure near the village of Östergarn, at Gannes 4, opened between 1987 and 1990, along the old main road to Kattammarsvik (present in the days of Dalman), about 700 m W of Östergarn church, was discovered by Dr. Lars Ramsköld. This locality weathers out numerous, in situ specimens of well-preserved shells very similar to those seen in old collections. Since most of the fossil collections of *prunum* were labeled 'Östergarn', this may well have been both the niveau and the Hisinger collecting site in the last century, although specimens occur elsewhere too. It occurs about 7–10 m below the limestone escarpment to the west, confirming its horizon within the Hemse beds. Gannes 4 may thus serve as a revised 'locus typicus restrictus' for *A. prunum*. This lies within a shoal to biostromal, proximal, or inner carbonate shelf setting, yet it is not specifically associated with biostromes, e.g., such as those described by Kershaw (1990, 1993) from Hemse 'C' strata of eastern Gotland. At Gannes 4 there are some phaceloid rugosans, but few shells of *A. prunum* are found directly with these, suggesting, along with incurved beaks indicating a loss of pedicle attachment, that adult shells were liberosessile.

Diagnosis [slightly expanded from Copper, 1977b]. Large, highly globose, elongate shells, averaging 25–26 mm wide, 22 mm deep, much longer than wide; rounded shoulder line; strongly curved lateral commissure; commonly highly arched, narrow U-shaped anterior fold in gerontic shells; small deltidial plates with apical foramen in neanic specimens, adult shells normally with foramen obscured by incurved, hypercline area.

Description. The species was previously redescribed, illustrated, and serially sectioned (Copper, 1977b), but the following additional data are available based on evaluation of large collections in the Riksmuseet from the probable type locality, Gannes 4. Shell width length and depth measurements bimodal or trimodal; widths 21–28 mm (maximum

29 mm, peak at 25–26 mm), lengths 28–33 mm (maximum 37 mm, peaks at 28, 33 mm), depths 17–25 mm (maximum 28 mm, peak at 22 mm). Young specimens (less than 10 mm wide) show an anacline area and slightly incurved beak with small deltidial plates, apical foramen, and a broad, shallow anterior fold. Deltidial plates are resorbed in larger shells, as the beak inflated and area curved into a hypercline position, obscuring the foramen. In some shells the foramen becomes transapical, but generally in adult shells the foramen is lost. A sharp demarcation of the fold (narrow, fold-parallel grooves on the vv) is not uncommon in gerontic specimens.

Remarks. Dalman (1828) mentioned already that the shell was very large, up to 35 mm long and 26 mm wide (similar to the statistical averages shown here in Fig. 83). This shell is almost as large as *Atrypoides gigantis* Jones 1981, described from the ?early Pridoli of Ellesmere Island, Arctic Canada, with widths in the 30–33 mm range. *A. prunum* is the largest species on Gotland: it is appropriately named, as many are the size and shape of large plums. Reports of this species have come from around the Baltic Basin and Podolia for more than a century (Eichwald, 1854, p. 63; Venyukov, 1899). The trimodal curve shown is based on multiple collections and may have limited significance, as the precise provenance of these is unknown. The Östergarn collections made in the 19th century were exchanged with many museums across Europe and are thus incomplete [nearly every major museum has a few specimens of this species]. If all of these came from a single fossiliferous locality, which is not impossible, then the trimodal curve may represent recruitment populations and reflect the age of the shells. This would mean that *A. prunum* achieved a mean adult age at 3–4 years. This could not be verified with seasonal growth interruptions, as these were rarely or only variably present.

The lack of an open foramen in most adult shells suggests the adult shell was free lying and not attached to the seafloor. Young shells show deltidial plates, a more orthocline area, and flattened shell, as seen in the variant called *Lingatrypa*. Slabs of nests of this species indicate that it lived in an umbo down, in vertical or nearly vertical position, despite a hypercline beak and closed foramen. This was also shown by Jones (1982) for Canadian Arctic species, probably weighted down by its thick umbonal shell and possibly also with the use of a partly atrophied pedicle, confirmed for Gotland material. A study of the relatively rare epibionts attached to the shell, predominantly auloporids or bryozoans, shows that these are primarily attached to the dv, near the anterior commissure. Where epibionts are present on the vv these are nearly always located on the strong U-shaped sulcus, at the commissure. Many specimens show geopetal infill. This observation, plus in situ specimens found on slabs, indicate that the shell was probably umbonally buried in soft carbonate muds at a steep angle to the surface, with only the middle to anterior and anterolateral margins protruding. This is also corroborated by the common observation of geopetal infilling; epibionts and endoliths are very rare, which would be expected if the shell were partly buried in life. *Atrypoides prunum* usually occur in micrites, pointing to a relatively low-energy, possibly lagoonal or sheltered, marginal to proximal, onshore shelf environment, confirmed by its geographically restricted domain on northeastern Gotland. Not a single specimen of the genus occurs in the western facies belt. Musteikis and Juskute (1999) interpreted the *Atrypoides* community in Latvia as more common in the offshore facies, opposite to that of Gotland, where it is in proximal, onshore facies. As a dominant element of the *Atrypoides* community, it is also associated on Gotland with solitary rugosans, syringoporids, and some phaceloid rugosans.

Nikiforova et al. (1985) recorded *A. prunum* from the uppermost Sokoi beds and the lower Grinchuk beds of the Malinovtsy Horizon from Podolia: this is within the lower Ludfordian *leintwardinensis* Zone, higher than the level at which it occurs in Gotland. Kaljo and Rubel (1982) reported *prunum* (sensu lato) from the Paadla (spanning the Hemse-Hamra/Sundre beds), and higher horizons in Estonia, for which there is no equivalent on Gotland, i.e., the lower Kuressaare (Ludlow) and Kaugatuma beds (Pridoli). This long range is at considerable variance with the data from Podolia and Gotland. The Estonian '*prunum*' may thus include several species, and statistical studies must be made to confirm this. The large, straight-hinged species *A. saaremaensis* Cooper and Rubel 1977, from the middle part of the Kuressaare beds of Estonia [= Hamra-Sundre beds, Gotland] is high Ludfordian, late Ludlow in age, lying within the *formosus* Zone, and thus substantially younger than *prunum*. The species *A. saaremaensis* does not occur on Gotland, probably because the equivalent Hamra-Sundre beds are in shallow 'faro' or coral-stromatoporeid 'atoll' facies (Kano, 1989; Samtleben et al., 2000).

Materials. Total 727 specimens [excluding materials examined in the British Natural History Museum, Lyon Museum, Paris Museum d'Histoire Naturelle, USNM]. '**Östergarn**' [probably = **Gannes 4**], uncatalogued collections Riksmuseet [Gamla collections: 226 shells], Br129881 [1], Br53100 [1],

Br42173-201 [28], Br42202-218 [17], Br42220-3 [4], Br123281-3 [3], Br103645-8 [4], Br42172 [1], Br42224-35 [12], Br124670 [1], Br129118 [1], Br129128-32 [5]; **Gannes 4**, revised locus typicus restrictus, small ditch outcrop W side of road, ca. 500 m N of Östergarn church [= SW52: 138; = SW90: 106]; **Gannes 2**, 'vagdike vid Ganne 550 m V om Östergarn Kirka', SJ Roma SO 627043:168288 [Ramsköld colln.:10]; **Gannberget 1** (= Östergarnsberget), 'nedanför Gannberget', Br58601 [1]; **Gannberget 2**, 'margel i en grup uppa berget', Br108851-6 [6]; **Grogarns 4**, beach locality, about 1300 m S of Grogarns, below large slumped units of Hemse strata, [SW21: 18]; **Grogarns 5**, beach locality outcrop halfway between Grogarnshuvud and Herrvik, [SW22: 52; former designated 'type locality' in Copper (1977b)]; '**Grogarns**, stranden', Br52920-3 [4]; '**Grogarn**, S om skana', Br627101 [1], Br62713-6 [4]; **Herrvik**, Östergarn sn., Br123284-7 [4]; **Brannklint**, Östergarn sn., Br46535-8 [4]; **Fersevik**, Br129133-48 [19], Br129121-7 [8, incl. two on one slab], Br129881, Br129210 [slab with 35 specimens]; **Katthammarsvik**, 'vid en brun nara hamnen', Br52991 [1]; **Hammaren**, Br108857-68 [13].

Atrypoides hemsea n. sp.

Pl. 27B, figs. a-j; Figs. 84, 85

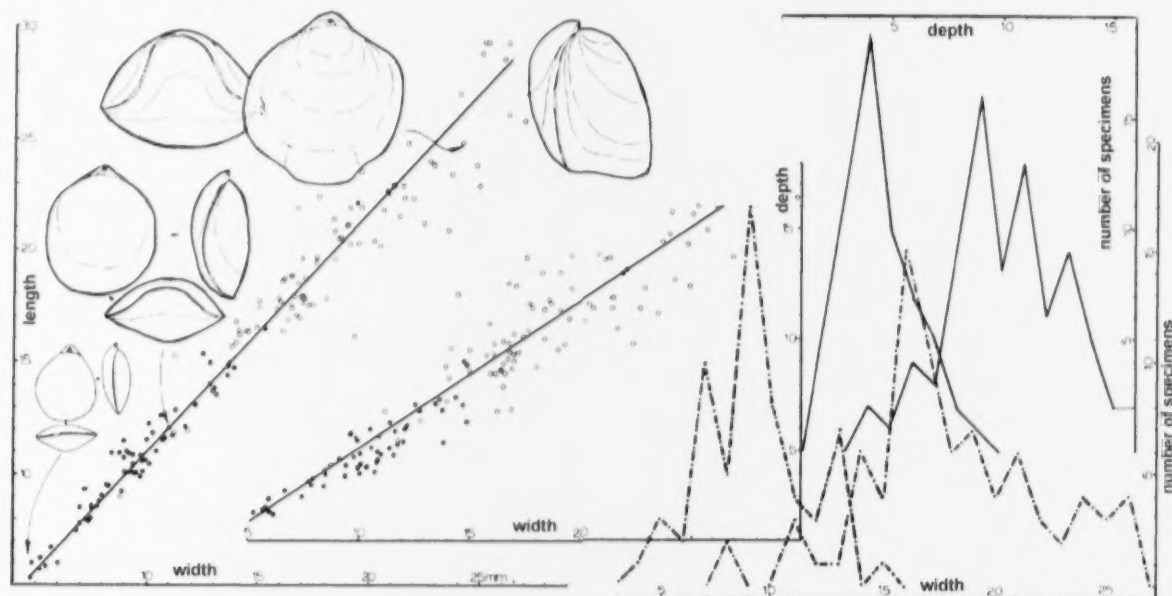
1975 *Lissatrypa* sp., Watkins, 1975, fig. 3 [reef locality, Ljugarn 1].

Type locality and stratum. The type specimens, the best preserved in the collections, are from Tänglings Hallar, a Hemse Formation reef and peri-reef setting, about 2 km due south of Etelhem village, from outcrops not exposed recently. This is designated the locus typicus. In the last years, abundant specimens have been available from **Ljugarn 1** (Laufeld, 1974b; see also Watkins, 1975), where dense concentrations of neanic, as well as rare large adult shells, occur in lenses within reefs and on immediate flanks of reefs in the lower part of the upper Hemse Formation, unit E (possibly high D?). 6J Roma SO 59150:75320 (Watkins, 1975, fig. 3). These are from the middle to upper *leintwardinensis* Zone, lower Ludfordian, Ludlow. The Ljugarn sample indicates that the old collections are biased by large, readily visible shells, and that neanic shells were probably overlooked, and misidentified. All the collections came from patch reefs, showing up on topographic maps as resistant hills (Klinte) or outcrops: the setting was a mid- to proximal, coral patch reef to mudmound habitat.

Diagnosis. Relatively flattened, averaging 19–23 mm, but up to 27 mm wide, slightly longer than wide shells; broad, low anterior fold; anacline adult area.

Description. Shells oval to rounded in outline; widths averaging 19–23 mm (maximum <27 mm), length exceeding width, depth peak at 14 mm; shells very smooth, with virtually no growth interruptions, growth lines; weakly indented shoulder line, hinge angles 100°–125°, averaging ca. 110°; blunt to weakly pointed beaks; orthocline area in young stages, anacline as adult shells; anterior fold relatively broad, wide and U-shaped in adult stages, nearly rectimarginate in young shells. Internally, small, solid deltidial plates; teeth very short, simple, located at sides of shell, dorsomedially to

Fig. 84. *Atrypoides hemsea* n. sp. Scatter diagrams (closed circles representing Ljugarn 1, upper Hemse beds, Ludlow, open circles remaining localities) and frequency curves (solid lines representing total, broken lines representing only Ljugarn 1). The two data sets indicate that the new collections represent especially the younger fraction of shells collected in nests from reefs at Ljugarn 1. Camera lucida sketches of typical shells, $\times 3$.



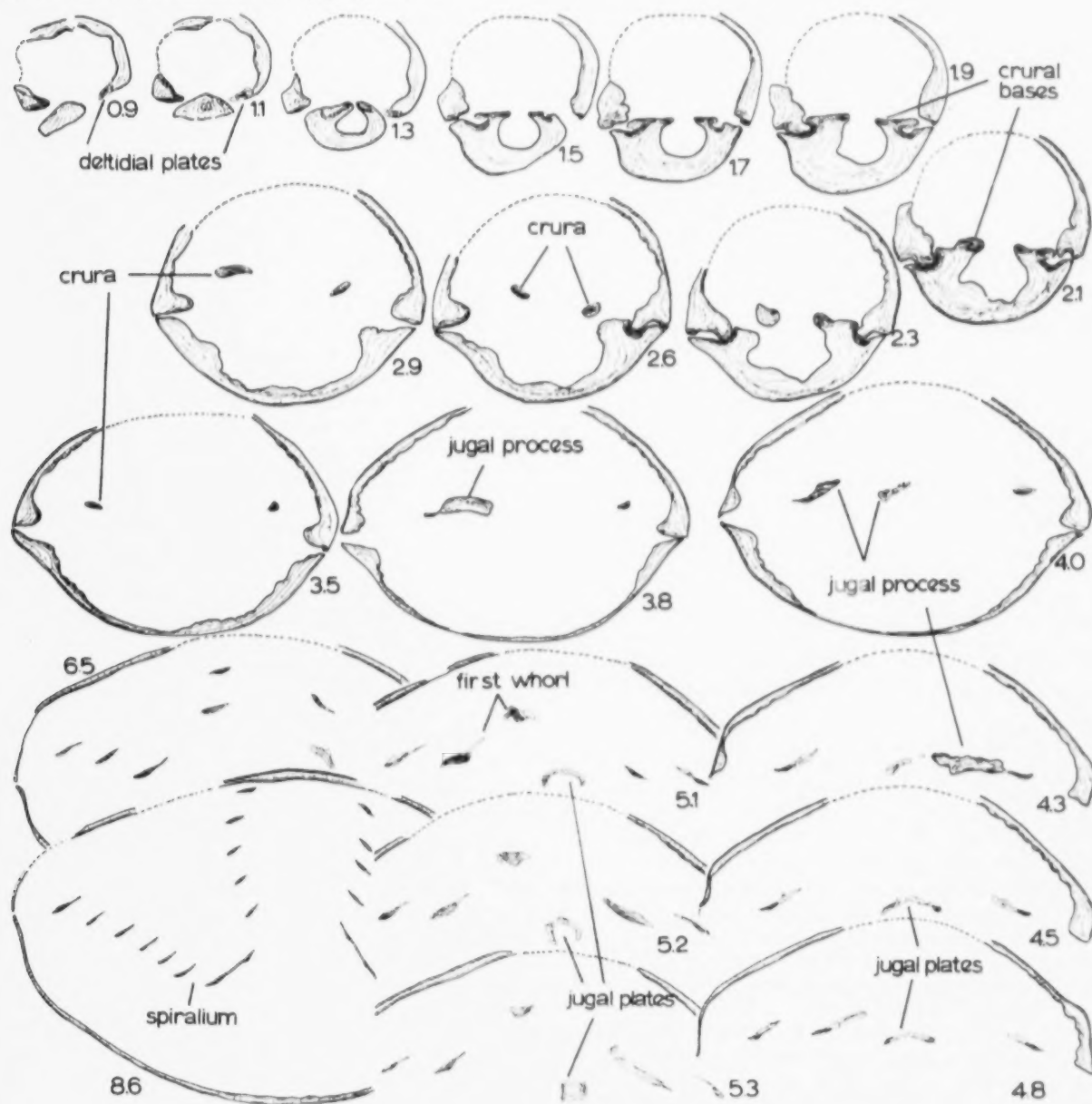
medially directed, solid, lacking lateral lobes; deep, rounded cardinal pit expanding into shell cavity; hinge plates thick; socket plates thin; long horizontal inner socket ridges; minute crural bases on inside margin; crura thick, short, unfeathered; jugal processes stubby, very thick on inner sides, straight to centre, then sharply curved 180°; jugal plates relatively thin, long ending in cylindrical to ring-like configuration; spiralia with about 6 whorls, dorsomedial.

Remarks. *Atrypoides hemsea* is readily distinguishable from *A. sulcata* and *A. prunum* in its flattened shape and moderate shell size. This species superficially resembles *Septatrypa* in its much less globose and more flattened vv with a wide fold, and its beak exposing deltidial plates in adult shells. However, serial sections clearly show the lack of dental cavities and dental plates typical of *Septatrypa*, and the cardinalia and brachidia demonstrate its *Atrypoides* character. Watkins (1975) assigned the shells, which he collected from Ljugarn 1, to *Lissatrypa*, but it lacks the distinctive hinge plate structure and teeth of that genus. Most of the shells at the Ljugarn locality occur in nests and tend to be small in size; larger adult shells are a rarity here, but others may have collected them because of their size. The shell has been found at several localities at the inland site Klinte, where their abundance within or near reefs points to a relationship similar to that discovered for *Atrypoides bioherma* in the Canadian Arctic by Jones and Narbonne (1984). It differs from the Canadian species in having deltidial plates, a dis-

tinct foramen, a flatter shell, and a gently rounded, instead of rectangular, fold. *Atrypoides hemsea* differs from *A. linguata* (Buch, 1835) from the Ludlow of Dlauha Hora [Kopana beds] in the Prague Basin by its wide (vs. rounded) shell and flat (vs. gently curved) anterior fold.

Materials. Total 485 specimens. Type locality, **Tänglings Hallar**, Etelhem sn., Br108467-9 [3], Br58741-65 [16], Br58766-89 [24]; **Ljugarn 1**, beach outcrop of small patch reef (see Watkins, 1975), [SW38: 66]; **Ljugarn**, Ardre sn., Br44500 [1]; **Lilla Rone**, järnvägskarning V om Lilla Rone, Lye sn., Br108463 [1], Br60458-65 [11]; **Bjars** traskbackar, Etelhem sn., Br59566-9 [4]; **Hageby** traskbackar, Etelhem sn., Br59585-90 [5]; **Sandarvekulle**, Fardhem sn., Br47037 [1], Br60476-7 [2], Br59776-97 [22], Br44656-62, 664-701 [46], Br108638-88 [51], Br44708-18 [11], Br44676-701 [26]; **Mannagarde** stenbruk, Lye sn., Br59748 [1], Br53005 [1], Br58713-22 [10], Br2489-91 [3], Br2514-20 [6], Br2498-99 [5], Br2451-52, 54, 61, 63-65, 67 [8], Br60460 [1], Br60740 [2]; **Lindeklint**, Br44449-67 [19], Br46852-90 [39], Br58628-58 [31], Br58686-7 [2], nordsidden Br59717-8 [2]; **Tonklint**, Lojsta sn., Br60460-1 [2], Br60469-71 [3]; **Mallgardsklint**, Levede sn., Br59749 [1], Br59750-1 [2]; **Gutensviken**, Östergarn sn., Br110870 [1]; **Lojstaklint**, Lojsta sn., Br46902-3 [2]; **Tänglings 4**, reefal limestone in road-cut, E side Highway 143, 1 km S Etelhem [SW34: 16]. Plus 48 unnumbered specimens from diverse localities listed.

Fig. 85. *Atrypoides hemsea* n. sp. Serial sections of large shell from Ljugarn 1, middle Hemse beds, Ludlow; note especially the jugal processes and complete recurvature of jugal plates, $\times 5$.



Family Septatrypidae Kozłowski, 1929
Subfamily Septatrypinae Kozłowski, 1929

Diagnosis. Small to medium-sized, smooth shells (rarely slightly corrugated), lacking fibrose ornamentation or filae; broad, wide, and usually high anterior fold; apical foramen; deltidial plates; delicate teeth, large dental cavities, and prominently thin dental plates; long, thin jugal processes.

Septatrypa (*Septatrypa*) Kozłowski, 1929
[= *Dubaria* Termier, 1936; = *Atrypopsis* Poulsen, 1943;
= *Rhynchatrypa* Siehl, 1962; = *Barkolia* Zhang, 1981]

Type species. *Septatrypa secreta* Kozłowski 1929, Podolia, Ukraine, Tajna beds, Lochkovian.

Range and distribution. Aeronian–Pragian, worldwide. The genus appears to occur first in the middle and late Llandovery of eastern Laurentia, e.g., such typical species as *Septatrypa julia* (Billings, 1862) from the Cybèle Member, and an unnamed species from the East Point Mbr., Jupiter Formation, Anticosti Island (Canada), and '*Atrypopsis*' from Greenland (Poulsen, 1943). Its last appearance is in the Pragian of Siberia (*Septatrypa gratsianovae* Alekseeva and Kulkov 1970).

Diagnosis. Smooth, or faintly corrugated, dorsibiconvex; protruding beak; small, orthocone–anacone area; apical to transapical foramen; deltidial plates exposed; broad, usually high, rectangular fold with flat tongue; internally thin shell wall; thin teeth, large dental cavities; distinctive long and thin 'dental plates'; cardinal process lacking in small cardinal pit; delicate hinge plates, subhorizontal inner socket ridges; geniculate crura; thin, ventrally arched jugal processes; long thin jugal plates, dorsally directed spiralia with usually fewer than 10, relatively widely spaced, narrow whorls.

Remarks. Four other genera, Ludlow *Dubaria*, Llandovery–Wenlock *Atrypopsis*, Ludlow *Rhynchatrypa*, and Wenlock *Barkolia*, are here regarded as junior synonyms of the Kozłowski genus named in 1929. There are various interpretations as to the validity of *Atrypopsis* versus *Septatrypa* (e.g., see Kulkov, 1967b) and Termier (1936), who described *Dubaria* from Ludlow strata of Morocco. I have sectioned specimens of *Dubaria* from Morocco and confirm this is internally the same as *Septatrypa*. Poulsen (1943) introduced the Llandovery–Wenlock genus *Atrypopsis* from Greenland, which cannot be distinguished from coeval *Septatrypa* from Anticosti Island, eastern Canada. Termier and Poulsen do not appear to have been aware of the description of this distinctive smooth atrypid from the Lochkovian of Podolia named earlier by Kozłowski, as neither cited previous descriptions. As a result, the genus *Septatrypa* remained uninvestigated internally until serial sectioning carried out by Siehl (1962), who introduced yet another new Silurian genus, *Rhynchatrypa*, for smooth shells from the Prague Basin and the Carnic Alps, without confirming earlier named taxa. The Wenlock genus *Barkolia* Zhang 1981 from Xinjiang, China, is said to possess 'mystrochial plates', but the illustrations of this structure are similar to the fusion of median septum and hinge plates, i.e., the so-called 'septalium–cruralium', seen in typical *Septatrypa* (e.g., as in *Septatrypa karlsoa* in this monograph). Biernat and Godefroid (1992) kept *Septatrypa* and *Dubaria* as distinct taxa. Internally, all the described genera are identical in possessing the same thin shell with large dental cavities and dental plates. The jugal processes have never been described formally for any of these genera, but Llandovery species from Anticosti are the same as Lochkovian *Septatrypa secreta* of Podolia, which have been sectioned for this study. The genus *Septatrypa*, as well as the subfamily Septatrypinae, are misnomers, since they lack a strong median septum, as implied by the name. The dorsal median septum is normally long (but sometimes also short, matching the extent of the muscle field which it divides), thin, and shallow, and appears 'prominent' in many specimens only because of the angle of serial sectioning and globosity of the dorsal valve. These features

give the appearance of a rhynchonellide-like 'septalium' or 'cruralium' in some specimens, but in fact there is no formal septalium or cruralium as seen in rhynchonellids. Indeed Havlíček (1961) identified several septatrypines initially as rhynchonellides, and Siehl (1962) called his rhynchonelliform genus *Rhynchatrypa*. Nevertheless, no fused inner socket ridges, e.g., a true septalium, exist in *Septatrypa*, such as known from rhynchonellides. In serial sections the shell, like that of the septatrypid subgenus *Hirciniscia*, commonly reflects the symmetry of rhynchonellid brachiopods. This is almost certainly convergent homeomorphy, as there is no indication that this is derived from a rhynchonellide that independently evolved calcified spiralia. A similar atrypid genus with apparent rhynchonellid homeomorphy is the Llandovery, very finely ribbed clintonelline *Beitaia* from China. *Beitaia* is puzzling in the sense that in serial sections there is a strong resemblance to *Septatrypa*; nevertheless, the two genera appear to be unrelated, and simply convergent in morphology. On the other hand, some brachiopods reported as *Septatrypa* in collections are known, from serial sections carried out for this monograph, to be true rhynchonellides (e.g., '*Septatrypa*' *subaequalis* Bassett, 1979), or athyridides. In the Urals (e.g., Mizens, 1981; Sapelnikov and Mizens, 1991), smooth septatrypines of Llandovery age have commonly been labeled as *Atrypopsis*, known from the Greenland work of Poulsen (1943); however, serial sections of Greenland and Anticosti material show no differences between Llandovery and younger smooth septatrypines, and all may be assigned to the senior genus *Septatrypa*.

Septatrypa is internally identical to the Wenlock–Ludlow genus *Hirciniscia* named by Havlíček (1960) in shape and internal morphology, and appears to differ only in the absence of weak corrugations ('ribs') located on the fold-sulcus. Even these ribs are faintly visible on otherwise smooth population variants of *Septatrypa karlsoa* and *S. petesvika*. The question of the status of *Hirciniscia*, however, is not fully settled, as details of the jugal processes are unclear. Some *Septatrypa* populations appear to have both smooth and ribbed versions present (e.g., *S. alumna*, *S. lissodermis*, *S. brekvice*; Havlíček, 1990). The ranges of the species within both genera overlap from Wenlock through Ludlow time. On Gotland, clearly corrugated forms are absent, although very faint undulations are visible around the commissure of some shells of *Septatrypa*, generally a rare genus here. *Septatrypa hircinaeformis* (Havlíček and Plodowski, 1974), an Early Devonian ribbed shell, also has ribs, suggesting that ribbing is a character trait within the *Septatrypa* group that may periodically recur, via repetitive appearance of an ancestral gene. Probably at best *Hirciniscia* could be defined as a 'rhynchonelliform' subgenus of *Septatrypa*, which is the status here allocated [see Copper, 2002b, p. 1466].

Septatrypa is relatively rare on Gotland, present only on the southwest side of the island. Four species have been described from glacial erratics of north Germany, and these are of uncertain stratigraphic origin. Only one species was found to be common on Gotland, *S. petesvika*, and this seems to occur in deeper water environments in the western facies of the Hemse Formation. The lowest occurrence on Gotland is in the Lower Visby beds, from which a single specimen, not serially sectioned, has been collected to date at Norderstrand. Reports of it in the Visby beds could not be con-

firmed, as serial sections showed that specimens labeled as *Septatrypa* were athyridides. The next occurrence is in the Slite beds at Stora Karlsö Island. Thus *Septatrypa* appears to be sporadic and rare in its presence, and to be facies bound.

In terms of its ecological occurrence, *Septatrypa* on Gotland was not found directly associated with reefs, stromatoporoids, corals, or calcareous algae, but instead occurs in calcareous shales or biostromal layers (coral thickets), interpreted as having formed in off-reef, deeper waters. Gotland *Septatrypa* were found primarily in the upper Slite Formation on Stora Karlsö, in the lower Hemse Formation (Petesvik), and as scattered occurrences in the Hamra beds. A single possible specimen is from the Upper Visby Formation (but this needs serial sectioning). In Podolia, its occurrence similarly is in off-reef beds. *Septatrypa* has not been confirmed in Britain or Ireland, although ?*Septatrypa beltiana* (Davidson, 1869) from Ireland, and the Telychian species *Meiodia ovalis supercedens* Williams 1951 from Wales, preserved as external and internal moulds, may be exceptions. Jones and Hurst (1984) suggested that Ludlovian *Septatrypa* (which they distinguished from Ludlovian *Dubaria*) were typically from cryptic habitats of biostromal and reefal environments. On Anticosti Island, *Septatrypa* occurs in both biohermal and non-biohermal habitats: in the East Point Member it is an abundant, but sporadic component of small bioherms, and it reaches maximum abundance in strata higher up in the Jupiter Formation, devoid of reefs or reef-forming biota. Thus there is no confirmation that *Septatrypa* was initially primarily a reef dweller: most species occurred on calcareous substrates in quieter water settings; none were found in very shallow water associations, such as in the Eke beds.

Species tentatively assigned. A total of 61 species and subspecies are listed, a number of uncertain affinity, and perhaps not even atrypids. Some 18 species from the Prague Basin have been described, with 9 species alone from the Dlouha Hora locality of the Kopanina Formation [12 species, if one adds the corrugated variants of the subgenus *Hirciniscia*!]. If this species assessment is correct, which seems most unlikely, the Prague Basin is the world centre for septatrypine diversity. The Harz area of Germany (Heritsch, 1930) contains a *Septatrypa* fauna identical to that of the Prague Basin. From glacial erratics of northern Germany, 4 probably synonymous species are described. By comparison, only 2 species are described from all strata in North America. Llandovery species number 13, Wenlock 13 spp., Ludlow 21 spp., Pridoli 6 spp., and Early Devonian 10 spp.

Atrypopsis absimilis Rybikina 1985, central Tuva, Dashtygo beds, Wenlock.

Septatrypa altaica Sennikov 1941, Altai Mountains, ?Lochkovian (see Khalifin 1948, p. 162).

Septatrypa alumna Havlíček 1991, Dlouha Hora, Prague Basin, lower Kopanina Fm., early Ludlow.

Septatrypa antiquata Nikiforova 1961, northern Siberian Platform, middle-late Llandovery.

?*Atrypopsis asiaticum* Menakova 1964, central Asia, middle-late Llandovery.

Lissatrypa aurita Sapelnikov 1960, eastern Urals, Marginalev Horizon, late Ludlow.

?*Rhynchonella beltiana* Davidson 1869, Cahireconree, County Kerry, Ireland, Wenlock.

?*Rhynchonella borealis* Heidenhain 1869, glacial erratics, N Germany, ?Ludlow.

Septatrypa brekvice Havlíček 1990, Jinonice-Praha, *nilssoni* Zone, lower Kopanina Fm., early Ludlow.

?*Rhynchonella Callawayiana* [sic] Davidson 1883 [also spelled 'callawayiana' on pl. 10, by Davidson], Walsall, Britain, Wenlock Shale, Wenlock [type lost, Cocks, 1978].

Septatrypa caprilupa Havlíček 1991, Kozolupy, Prague Basin, lower Kopanina Fm., early Ludlow.

?*Atrypopsis chondelensis* Rybikina 1985, Tuva, Alash beds, ?Rhuddanian, Llandovery.

Septatrypa elliptica Xu 1979d, Nandan, Guangxi, Tangxiang Fm., ?Lochkovian, Early Devonian.

?*Atrypa fabula* Barrande 1879, Konieprus, Prague Basin, Pragian.

Septatrypa gratsianovae Alekseeva and Kulkov 1970, Gurevsk, Kuznetsk Basin, Malobachat beds, Pragian [in Alekseeva, 1970].

Terebratula harpyia Barrande 1847, Dlouha Hora, Prague Basin, Pridoli Fm., Pridoli [see also Kayser, 1878, pl. 24, fig. 14, for occurrence in Thüringen].

Atrypa sappho var. *hircina* Barrande 1879, Kolednik, Prague Basin, lower Kopanina beds, early Ludlow.

Dubaria hircinaeformis Havlíček and Plodowski 1974, Skalce, near Menany, Prague Basin, early Lochkovian.

Septatrypa ?incerta Wang 1984, western Hubei, Shamao Fm., Wenlock [see also Grabau, 1926].

Athyris julia Billings 1862, Anticosti Island, Canada, Jupiter Fm., Telychian, Llandovery.

Septatrypa karlsoa n. sp., Karlsö, Slite beds, Wenlock.

Dubaria lantenoisi Termier 1936, Belbégar, Morocco, Ludlow.

Terebratula latisinuata Barrande 1847, Praha-Klukovice, Prague Basin, Pridoli.

Atrypopsis legrinus Kulkov 1974, Kamyshehensk, N Altai, Yavorski beds, Telychian, Llandovery.

?*Atrypa lindströmi* Venyukov 1899, Studentitsa, Podolia, Kitagorod beds, Wenlock [see Nikiforova, 1954, p. 122, for dental plates].

Lissatrypa linguifera Khodalevich 1939, Ivdel region, Urals, Striatov beds, Ludlow.

Septatrypa lissodermis Havlíček 1991, Kozolupy, Prague Basin, upper Motol Fm., Telychian, Llandovery.

Septatrypa thetis var. *localis* Khodalevich 1951, Ivdel region, Urals, Saum Horizon, Lochkovian.

Septatrypa magna Nikiforova 1961, Moiero River, north Siberian Platform, middle-late Llandovery.

Septatrypa magna forma *pentagonalis* Nikiforova 1961, Moiero River, Siberian Platform, Llandovery.

Terebratula megaera Barrande 1847, Kolednik-Jarov, Prague Basin, upper Kopanina Fm., late Ludlow.

Dubaria megaerella Plodowski 1971, Cella, Austria, Pridoli.

Dubaria megaeroides Johnson and Boucot 1970, Ikes Canyon, Toquima Range, Nevada, Tor Limestone, Pridoli.

Septatrypa petesvika n. sp. Petesvik, western Gotland, Hemse beds, early Ludlow.

Rhynchonella pinguis Haupt 1878, glacial erratics, N Germany, 'Graptolithenkalk' [cf. Roemer, 1885], Ludlow.

- Lissatrypa plena* Sapelnikov 1960, eastern Urals, Marginalev Horizon, late Ludlow.
- Atrypopsis pseudothetis* Rzhonsnitskaya 1968, Gurevsk, Kuznetsk Basin, Krekov beds, Pragian.
- Atrypopsis pseudovarians* Fu 1982, Qinling Mountains, China, ?Wenlock.
- ?*Dubaria guangyuanensis* Sheng 1975 [nomen correctum from *guangyuanensis*], Guangyuan, South China, Aeroonian [nomen correct.], Llandovery.
- Atrypopsis reclinis* Rubel 1970, Hilliste, Estonia, Juuru Horizon, Rhuddanian, Llandovery.
- Dubaria rongxiensis* Wan 1978, Rongxi, Sichuan, S China, Wenlock–Ludlow.
- Dubaria saphina* Havlíček 1991, Kolednik, Prague Basin, lower Kopanina Fm., early Ludlow.
- Atrypopsis severnensis* Jin, Caldwell, and Norford, 1993, Hudson Bay lowlands, Severn River, Ontario, Attawapiskat Fm., Telychian, Llandovery.
- Atrypa sinuata* Venyukov 1899, Kitaigorod, Podolia, Kitaigorod Fm., Wenlock.
- ?*Septatrypa subanalogia* Rybnikova 1967, Akniste, Latvia, Wenlock.
- ?*Terebratulula subcurvata* Münster 1840, 'Orthoceratitenkalk', Elbersreuth, N Germany, ?Ludlow.
- Lissatrypa sublima* Sapelnikov 1960, eastern Urals, Striatov Horizon, early Ludlow.
- Septatrypa subsecrta subsecrta* Plodowski 1976, Eggenfeld, Austria, Pridoli.
- Septatrypa subsecrta trapezoidalis* Plodowski 1976 [as for subsp. *subsecrta*].
- Rhynchonella succisa* Richter 1866, Thüringen, Germany, 'Tentakulitenschiefer', Ludlow.
- Septatrypa sulcificata* Havlíček 1991, Kozolupy, Prague Basin, lower Kopanina Fm., early Ludlow.
- ?*Meifodia ovalis supercedens* Williams 1951, Llanerchgoch, Wales, Telychian, Llandovery.
- Atrypopsis suprareclinis* Sapelnikov and Mizens 1982, E slopes central Urals, Elkin beds, Wenlock.
- Dubaria tenera* Nikiforova and Modzalevskaya 1968, Ribnoi River, Omnutakh, Siberia, Telychian, Llandovery.
- Terebratulula thetis thetis* Barrande 1847, Konieprus, Prague Basin, Pragian.
- Septatrypa thetis localis* Khodalevich 1951, Urals, late Lochkovian – early Pragian.
- Rhynchonella triangularis* Haupt 1878, erratics, N Germany, 'Graptolithenkalke', Ludlow.
- Rhynchonella* (?) *trilobula* Roemer 1885, 'Rostock', glacial erratic, ?Ludlow [misspelled *trilobata* in text, see pl. 9].
- Barkolia typica* Zhang 1981, Hongliuxia Formation, Balikun county, Xinjiang, Wenlock.
- Atrypopsis varians* Poulsen 1943, Offley Island Fm., ?late Llandovery–Wenlock.
- Atrypa verna* Barrande 1879, Dlouha Hora, Prague Basin, Kopanina Fm., late Ludlow.
- ?*Terebratulula vultur* Barrande 1847, Prague Basin, Ludlow.
- Atrypa zelia* Barrande 1879, Luzec-Lodenice, Prague Basin, Motol Fm., Wenlock.

Species deleted.

'*Septatrypa*' *subaequalis* Bassett 1979, Slite beds, *Pterygotus* layer, Wenlock, Gotland [my serial sections of specimens

from the type locality show that this is a rhynchonellid: see Appendix]. In addition, serial sections undertaken from Barrande collections at Lyon labeled under the name *harpyia* (see above list) show great similarities to the Bassett species, and may also be rhynchonellids. However, Havlíček (1991, p. 187) shows serial sections of '*Dubaria harpyia*' that make assignment to *Septatrypa* possible, although no spiralia are demonstrated. *Spirigerina cordata* Lindström 1861 (p. 363), 'Gannarfve i Fröjel i sandhaltig kalkskiffer', Slite beds, probably = *Plagiorhyncha*, and perhaps = *Plagiorhyncha subaequalis*.

Septatrypa secreta Kozłowski, 1929

Figs. 86, 87

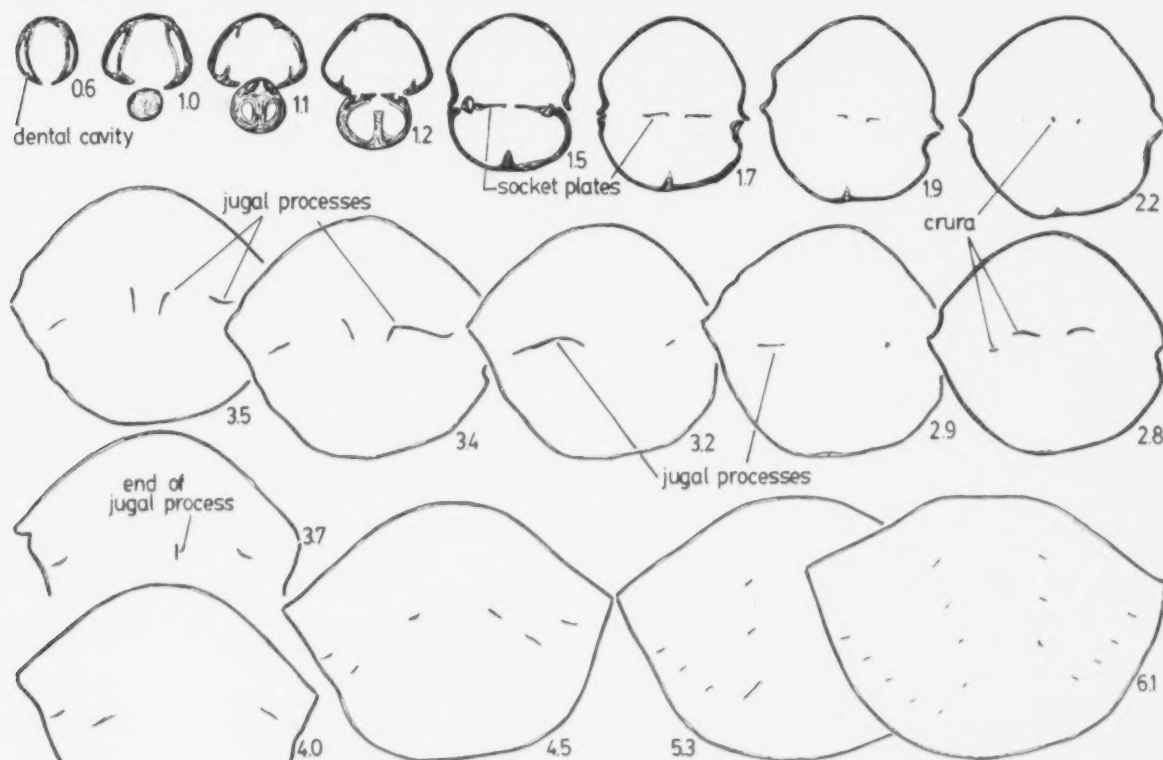
- ?1869 *Rhynchonella borealis* Heidenhain, p. 157, pl. 1, fig. 9.
- ?1885 *Rhynchonella* sp., Roemer, p. 120, pl. 9, figs. 15a–c.
- 1906 *Atrypa thetis* Barrande, Siemiradzki, pl. 7, figs. 11a–d.
- 1929 *Septatrypa secreta* Kozłowski, p. 17, pl. 9, figs. 18–24.
- 1985 *Septatrypa secreta*, Nikiforova, Modzalevskaya, and Bassett, p. 44–45, pl. 11, figs. 9–11.

Type locality and stratum. Borshechov Horizon, Tajna beds, Lochkovian, Podolia (Nikiforova et al., 1985, p. 44).

Remarks. The external morphology has been adequately illustrated by Kozłowski (1929) and Nikiforova et al. (1985). No statistical information is available on variation in size and shape in the Podolian type species. Topotypic material sent by Dr. T. Modzalevskaya (see Modzalevskaya, 1968), and collected by me in the field in 1993 (with the help of Dr. V. Gritsenko), has enabled a direct internal comparison of this species to those from Gotland. The serial sections illustrated by Nikiforova et al. (1985) were idealized, and do not show the nature of the crura, jugal processes, and spiralia. There is no dark line in the centre of the septum as indicated by Nikiforova et al. (1985), and the septum is no different than any other known for the atrypid group. Nikiforova et al. (1985) remarked that the septum is highly variable, which is here confirmed. However, a true rhynchonellid septalium, formed by bridging the inner socket ridges and septum, is absent. The median septum is variable only in the sense that its appearance depends on variable development of shell wall thickness, the angle of serial sections, and (or) the globosity and old age of the shell. Serial sections of specimens from the same population show a range of septum variation from those that ostensibly show a 'septalium' to those that lack one. A dorsal median septum exists and is usually, but not always, well developed. No distinction is possible in the atrypids between a so-called 'true' septum (a partition which exceeds the muscle field) and myophragm (which divides the muscle field). In that sense, the genus is misnamed because the septum is not diagnostic.

The nature of the hinge structure and the crura and jugal processes are unique to the genus, as shown here for the first time in serial sections and the reconstruction therefrom. In *Septatrypa secreta* (and other species sectioned) the hinge plate is thin and delicate, and the inner socket ridge is horizontal, extending almost as a thin shelf across the valve, but not fused. The crural bases are long, extremely thin, and give rise to arched and slender crura leading to the sides. The crura also typically appear to be geniculated, i.e., in-

Fig. 86. *Septatrypa secreta* Kozłowski, 1929. Borshchov Horizon, Tajna beds, Lochkovian, Early Devonian. Serial sections demonstrating the crura, jugal processes, and spiralia of a specimen from the type horizon, $\times 5$.



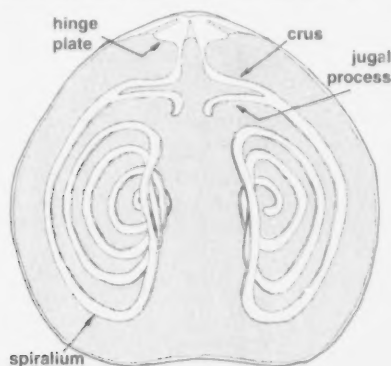
stead of curving gently outwards, they are first directed medially, then bend sharply to the sides. Feathering of crura appears absent or poorly developed. The jugal processes almost repeat the trajectory of the crura, but in reverse, being arched and thin, and terminating in quite long, trailing, vertical jugal plates in the centre. There are about 4-6 spiral whorls, and these are dorsally and slightly medially directed. Havlíček (1991) stated that there is a fused jugum present in Llandovery forms: this cannot be verified, but certainly does not exist in Llandovery specimens from Anticosti sectioned

by me. *Septatrypa julia* (Billings, 1862) from Llandovery strata of Anticosti has separated jugal processes and is internally almost identical to the Podolian type species. If the glacial erratic species *Rhynchonella borealis* Heidenhain (1869) is *Septatrypa*, the type species name may have to be altered, or the name *borealis* dropped as a nomen oblitum.

Septatrypa karlsoa n. sp.

Pl. 26D, figs. a-j; Figs. 88-90

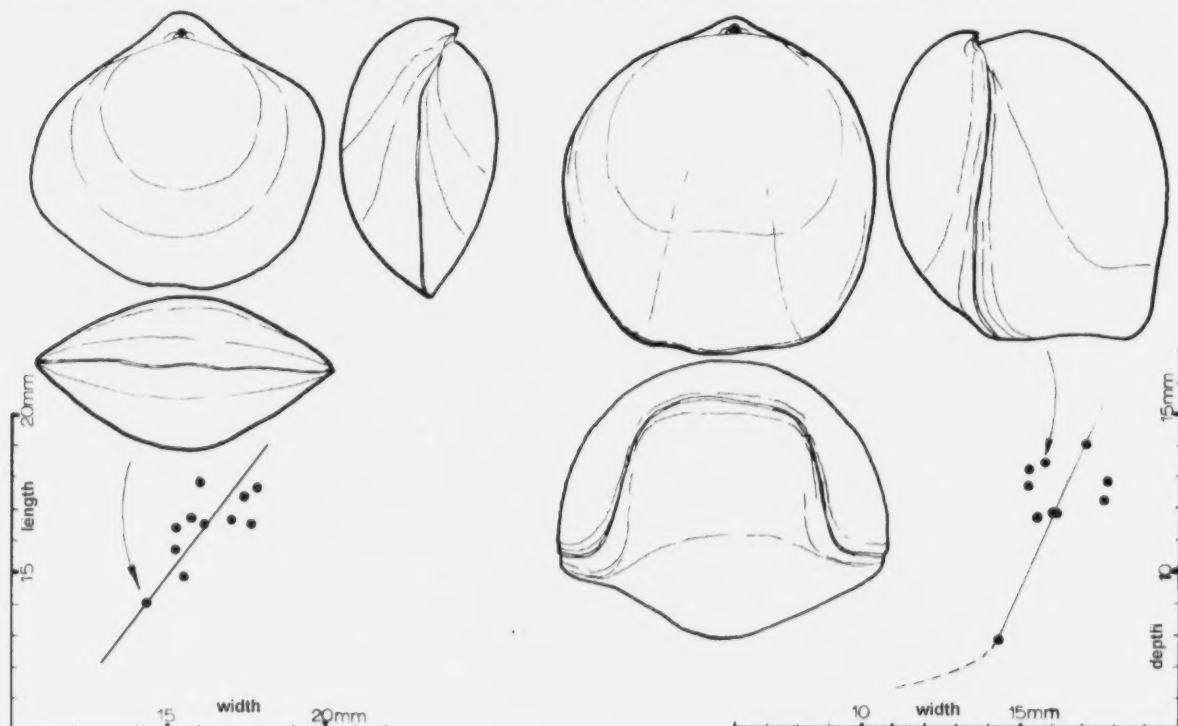
Fig. 87. *Septatrypa secreta* Kozłowski, 1929. Reconstruction of serial sections from Fig. 86, demonstrating the geniculated crura, thin and delicate jugal processes, and spiralia. Borshchov Horizon, Tajna beds, Lochkovian, Early Devonian, $\times 8$.



- ?1878 *Rhynchonella pinguis* Haupt, p. 42, pl. 2, fig. 13 (erratics, northern Germany).
- ?1885 *Rhynchonella* sp., Roemer, p. 120, pl. 10, figs. 15a-c (Lerchenborn erratics, Germany).
- ?1890 *Rhynchonella beltiana* Davidson, Gagel, p. 60, pl. 4, figs. 14a-c ('Schönau', glacial erratics, N Germany).
- ?1890 *Rhynchonella glassii* Davidson, Gagel, pl. 1, figs. 31a-b ['Wehlau', glacial erratics, N Germany].

Type locality and horizon. Stora Karlsö Island, west coast of Gotland, bluff and low cliff about 10 m high, at Ramroir 1, S of Lerberget, ca. 300 m N of Stornasen, 400 m S of lighthouse, 61 Visby SO 53200:29780 (= SW109; for illustration of locality see Munthe et al., 1927a, fig. 20). A locus typicus restrictus could be Lerberget 4, the probable source of the holotype Br124739, but at Ramroir 1 the species is more common. Bedding plane and vertical bluff surfaces at the type locality consist of soft-weathering calcareous shales outcropping at beach level on the west side of Stora Karlsö.

Fig. 88. *Septatrypa karlsoa* n. sp. Statistical variation in scatter diagrams: data pooled from Stora Karlsö localities, Slite beds, middle Wenlock. Camera lucida sketches of immature and mature shells showing great variation in shell shape with size.



These shales are part of the Slite Formation, probably the upper Slite beds (unit G), about 3–5 m below the resistant Halla–Klinteberg limestones on the island. The stratigraphic level of this part of the Slite Formation is probably in the early Homerian, i.e., the *lundgreni* Zone. The type horizon is the shales directly underlying the 'beet reef' mass occurrences of the large solitary rugosan *Dokophyllum*, and within the phaceloid coral biostromes. Associated fauna consists of common *Plectatrypa parimbricata*, common pancake-shaped stromatoporoid and heliolitid colonies, halysitids, and rare large phaceloid rugosans. *Septatrypa* is a relatively rare element of the biostromal fauna: it is not present 3–4 m down the Slite beds, where *Oglupes davidsoni* is abundant, and corals are rare. Its location suggests an offshore, distal shelf setting, but in relatively coral-rich biostromes above normal wave base. It is absent in the proximal shelf and patch reef facies of the Slite beds on Gotland to the east.

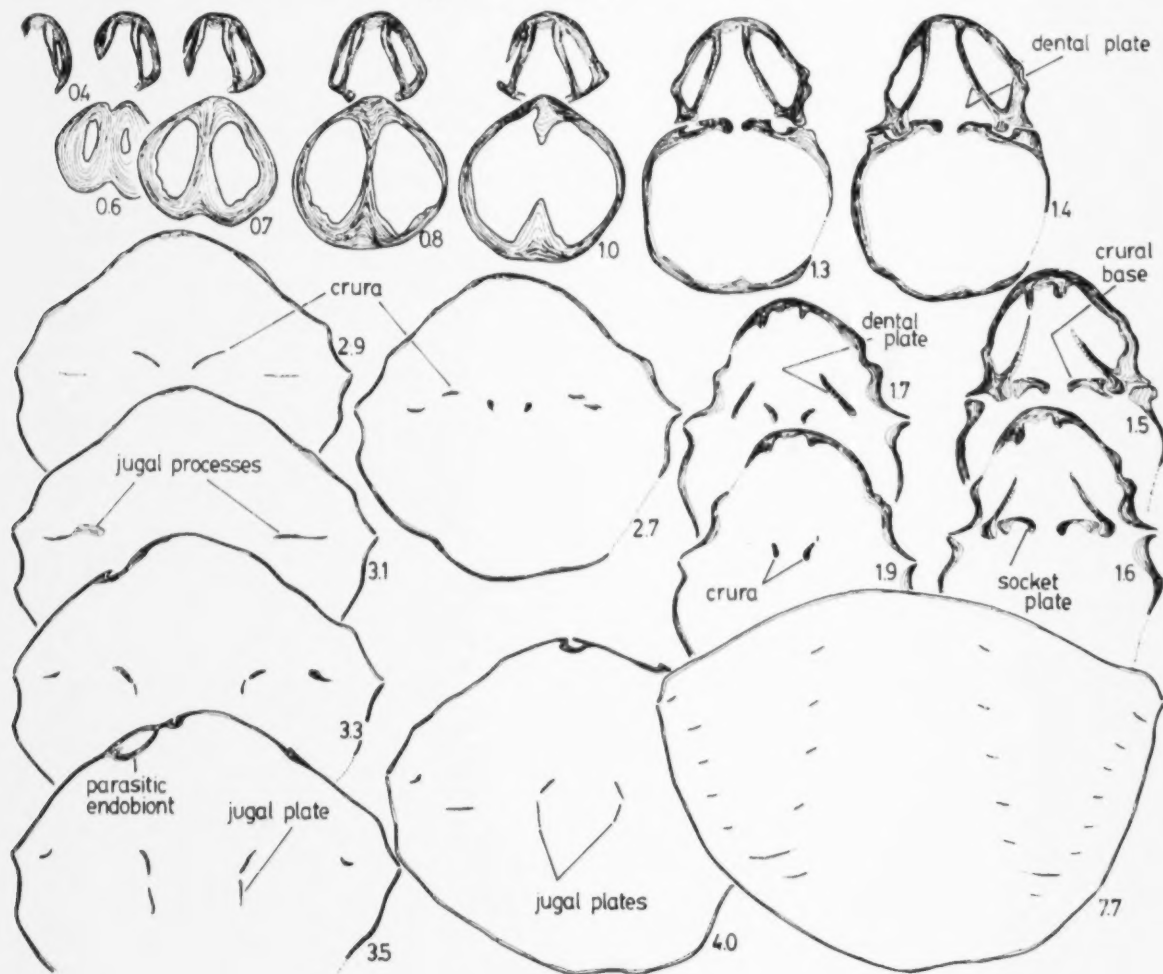
Diagnosis. Relatively large, 15–18 mm wide, globose septatrypine; high, squared anterior fold; pinched ventral umbo; pedicle callist present; curved, thick dental plates; spiralia with ca. 7 whorls.

Description. Relatively large sized, dorsibiconvex; vv moderately inflated, dv more convex than vv; 15–18 mm wide; maximum width posterior to mid-shell; about as wide as long; 11–14 mm deep; rounded hinge corners; pinched ventral umbo; hypercline area; strongly incurved beak; small, expanded foramen; minute deltidial plates to side; abrupt geniculation of lateral commissure with development of broad, high, flat anterior fold. Internally, tapering, V-shaped

pedicle cavity; pedicle callist developed; small deltidial plates; prominent, ventrally thickened dental plates diverging at V-shaped angles [mimicking 'mystrochial plates']; large, elongate, wide dental cavities, flanked by 'dental plates'; teeth short, lacking lateral lobes; dorsal median septum prominent; hinge plates very thin; socket plates delicate, subhorizontal; crural bases small, elongate, curved laterally to thin plates, unfeathered or weakly feathered; jugal processes short, with thick inner ventral portion, curving dorsally and terminating in thin, vertical jugal plates; spiralia with fewer than 7 whorls, dorsally directed.

Remarks. Specimens are rare at every outcrop of the Slite shales examined on Stora Karlsö, and this large species occurs nowhere else in the Gotland area, or the Baltic Basin, as far as could be determined. Preservation shows that most specimens are hollow or largely infilled with calcite spar, and a thin layer of micrite at the base of the pedicle valve. The stable, probable life, position was vv down, a position in which all in situ shells were observed: moreover, the pedicle opening is minute and probably played only a minor role in pedicle attachment. *Septatrypa karlsoa* is distinct from *S. petesvika* in its much larger size (nearly twice that of *S. petesvika*), globosity, and highly arched anterior fold: it also has a thin pedicle callist, missing in other Gotland species. It differs from the type species *Septatrypa secreta* Kozłowski 1929 in its thicker and larger shell, and wider apical angle. Young specimens of *Septatrypa karlsoa* could be mistaken for *Lissatrypa* in having a rounded, biconvex shell lacking an anterior fold; their internal structure is entirely different.

Fig. 89. *Septatrypa karlsoa* n. sp. Serial sections, paratype Br48813, Stora Karlsö, Slite beds, middle Wenlock. Note the pinched ventral umbo around the lateral commissure, the general lack of support of the hinge plate by a median septum, except in apical stages (less convex shells sectioned never show a 'septalium'), the diverging dental plates that could be mistaken for 'mystrochial plates', presence of parasitic endosymbiont encased by atrypid shell on vv, $\times 5$.



Several species of probable or possible septatrypines have been described from glacial erratics of North Germany by Roemer (1861, 1885), Heidenhain (1869), Haupt (1878), and Gagel (1890), but the specimens appear to have been lost, and the descriptions and figures are inadequate to determine

Fig. 90. *Septatrypa karlsoa* n. sp. Reconstruction of serially sectioned specimen, Fig. 89, Br48813, Stora Karlsö, Slite beds, middle Wenlock, $\times 5$.



size and shape. These species are regarded as nomina oblita here, until the type material can be found. Specimens most similar to this species were discovered in glacial erratics from Holland by Gagel (1890), who discovered a shell of the same size and very high angular fold: the Gagel species was cited as '*Rhynchonella beltiana*' Davidson 1853, an obscure species, possibly a rhynchonellid, from Wales. It is possible that these erratics were thus derived from the W coast of Gotland, since the genus is absent in the centre and east side.

Materials. Total 11 specimens from the Slite beds: the new collections made were mostly derived from a single horizon about 20–30 cm thick, below the '*Omphyma*' [= *Dokophylum*] biostrome of large, fat, conical solitary corals, and a few metres below the Klinteberg reefal facies. **Stora Karlsö.** Br48813 [sectioned specimen] and Br48814: **Ramroir 1** [restricted type locality because the species is more abundant here], shaly units in coral thicket facies, below solitary coral

units, low bluffs on west coast of Stora Karlsö S of Lerberget [SW109: 4]; **Lerberget 4**, bluffs directly N of slumped cliff, unit immediately below 'Omphyma' beds [SW111: 1, and Br124739-40:2 shells]; **Lushålet 1**, shales at base of cliff, directly below lookout and lighthouse, Stora Karlsö; *Septatrypa* here occurs in a Rasenriff setting of abundant, broken, pencil-thick phaceloid rugosans [SW112: 1].

Septatrypa petesvika n. sp.

Pl. 29A, figs. a–s; Figs. 91, 92

?1878 *Rhynchonella triangularis* Haupt, p. 69, pl. 2, figs. 9a–c.

Type locality and stratum. Tidal flat exposures in the middle and northern part of the bay at Petesvik, Hablingbo sn. (Jaanusson, 1986). The locality was apparently well known in the 19th century, and described by Schmidt (1859), Lindström (1861), and van Hoepen (1910). Tidal flat outcrops occur around a cluster of small fishing huts, and for about 500–700 m NNW, where greyish blue calcareous shales and argillaceous limestones of the lower Hemse beds (?unit A) crop out on bedding plane surfaces. There is no mention of this fossiliferous locality in Munthe et al. (1927b). Two attempts were made to rediscover the exact location of the *Septatrypa* locality on Petesvik Bay in 1974 and 1990 on the basis of the description of van Hoepen (1910). Very fossiliferous beds were found to occur at the northwest end of the bay, but these produced only a single shell of this species [Sandskallen 2], although there were abundant, small *Atrypa purchisoni* and a rich, dwarfed *Cyrtia trapezoidalis* – 'Howell-ella' plicatellus fauna. The *Septatrypa* fauna from old Petesvik collections must have been clustered, possibly a single nest, and this location was not rediscovered. For the associ-

ated fauna, see Lindström (1882). This locality also yielded common, small *Leptaena*. This level appears to lie within the upper part of the *nilssoni* Zone, early Ludfordian, early Ludlow. Jaanusson (1986) noted that the Lilla Hallvards 4 locality yielded a similar fauna, but this produced no *Septatrypa*. *Septatrypa* only occurs locally in the SW facies belt of the Hemse Formation, thus in a distal shelf, deeper marine facies without corals or algae, typified by a relatively dwarfed brachiopod fauna and common graptolites and trilobites.

Diagnosis. Small, somewhat flattened, biconvex; average widths 8 mm, longer than wide; ovoid-subtriangulate; narrow hinge angle; spiralia fewer than 5 whorls.

Description. Small, weakly biconvex, somewhat flat shell; widths 7–8 mm (average 8 mm), maximum width at mid-shell or anteriorly; longer than wide, lengths 8–10 mm (average 9 mm); depths 5–7 mm; shell shape ovoid to somewhat squared, depending on fold; hinge angles narrow, 85°–95° (average about 90°); shoulder line straight or slightly convex; no hinge corners present; beak protruding slightly; short anacrine area; foramen commonly transapical, except in earliest growth stages; deltidial plates long, narrow; lateral commissure relatively straight until the sharp and angular with a flat or even W-shaped fold. Internally, large apical dental cavities; teeth with thin, flat dental plates tilted to the sides dorsally; teeth short, stubby, dorsomedial in direction; cardinal pit small, rounded, lacking cardinal process; dorsal septum strong; socket plates thin; inner socket plates delicate; minute crural bases; crura thin, rounded, curved strongly in middle of shell; jugal processes arched in U-shape, facing dorsally, terminating in long trailing jugal plates, with slight curve at their ends; spiralia mediodorsal with 4 whorls.

Fig. 91. *Septatrypa petesvika* n. sp. Scatter diagrams and frequency curves compiled from Petesvik locality, Hemse beds, western facies, early Ludlow, very likely a single population at one site; width peak at 8 mm, depth peak at 5–6 mm; camera lucida drawings of three types (see photographs, Pl. 29).

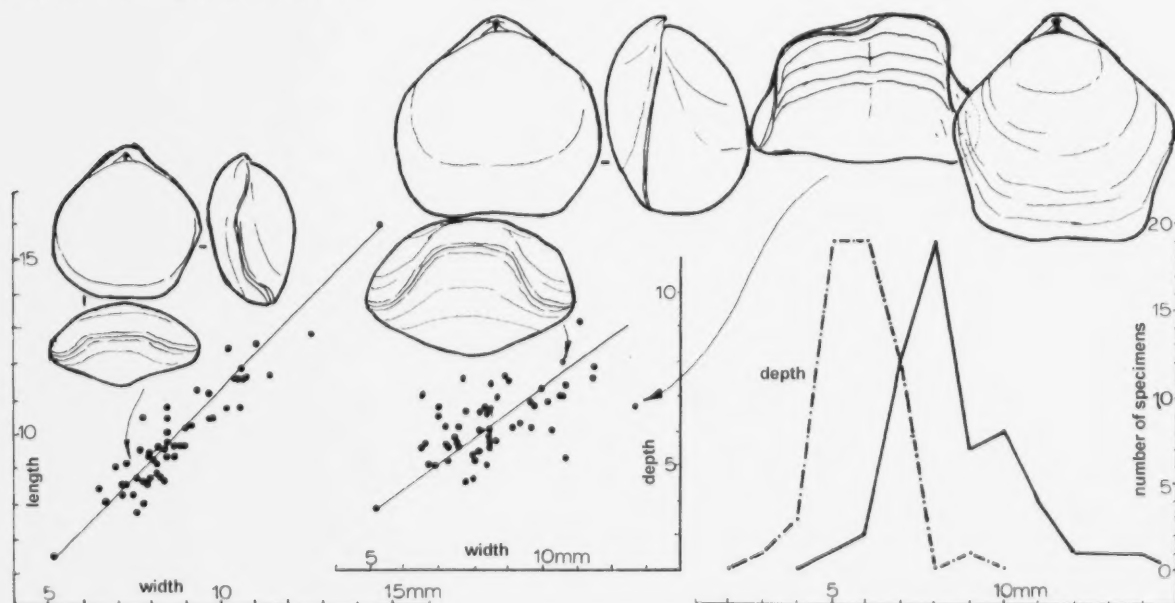
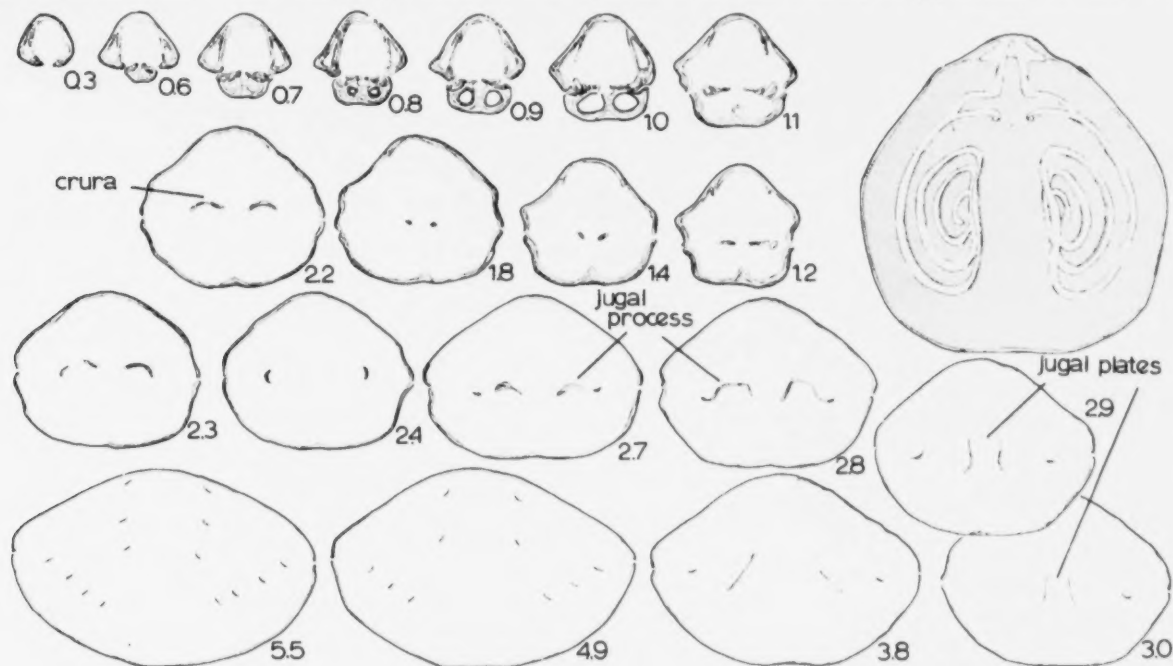


Fig. 92. *Septatrypa petesvika* n. sp. Serial sections and reconstruction of dorsal valve interior of paratype Br108461, 'Petesvik', Hemse beds, western facies, early Ludlow; note the appearance of a false 'septalium' in this shell, relatively sharp geniculation of crura; all $\times 5$.



Remarks. The small size (half the size *Septatrypa karlsoa*), and ovoid, subtriangulate, flattened shape, with narrow hinge angle, distinguish this species from others described on Gotland. It is substantially less globose than *S. secreta* (Kozłowski, 1929), although some members of the population begin to approach that convexity. The glacial erratic species from northern Germany, *Rhynchonella triangularis*, described by Haupt (1878), is remarkably similar in shape, very likely referable to *Septatrypa* and possibly conspecific. Since the internal structure was not described by Haupt and cannot be verified as belonging to *Septatrypa*, and the type material appears to be missing, it is left as a nomen oblitum, and this new species is erected. *S. petesvika* resembles neanic shells of late Ludlow *S. megera* (Barrande, 1847), but does not reach the bisulcation and adult large sizes shown by the Prague Basin species.

Materials. Total 60 specimens, all from the lower Hemse Formation, western shaly facies and nearly all from the type locality. **Petesvik 1**, type locality (material labeled in collections as 'Petesvik', with no more precise data: refer to Jaanusson, 1986), Br44407-17 [13], Br44420-48 [28], Br59763 [1], Br108389-405 [17]; **Sandskallen 2** bedding plane outcrops on NE side of Petesvik Bay [SW100: 1 shell]; **Lilla Rone**, järnvägsgräning V om, Lye sn., Br108461-2 [2]. Other localities with a similar dwarfed brachiopod fauna lacked *Septatrypa*, e.g., Smisssarve 3, Smisssarve 4, Sandskallen 3.

Septatrypa (Hircinisca) Havlíček, 1961

Type species. *Atrypa Sappho* [sic] var. *hircina*, Barrande 1879, Koledník, Prague Basin, Kopanina beds, lower Ludlow.

Range and distribution. Wenlock-Pragian, ?Emsian; Czech Republic, Urals, Siberia, South China, ?NW Canada.

Diagnosis. *Septatrypa* with well-developed corrugations ('ribs') on the distal, anterior shell surface, especially near the commissure.

Remarks. *Hircinisca* is identified exclusively by the presence of corrugations (not true 'ribs', or costae) along the anterior commissure, giving the shell a rhynchonellid shape and appearance. Internally, the shell is that of *Septatrypa* sensu stricto, with atrypoid spiralia. The Barrande (1879) species *Atrypa sappho* var. *hircina* with such corrugations was first identified as a rhynchonellid by Havlíček (1961), as they externally resemble some nearly smooth *Plagiorhyncha*. Development of faint anterior corrugations also occurs as a population variant within some *Septatrypa* species, and a gradient exists between these 'ribbed' and 'unribbed' species, suggesting that it is probably best to regard *Hircinisca* no higher taxonomically than as subgenus, or just population variants with corrugations. The Caradoc genus *Idiospira*, the oldest septatrypine, also shows some smooth and some corrugated variants within populations, so this trait is ancient. *Septatrypa* and *Hircinisca* have the same geologic range, from Wenlock through Early Devonian time, although ribbed forms seem absent in Llandovery strata, except the uppermost. *Hircinisca* is unknown from Gotland, although some Gotland *Septatrypa* show the development of weak corrugations on the smooth shell that make them resemble *Hircinisca*. Hede (1917, pl. 1, figs. 15-19) illustrated a Barrande Ludlow species called '*Atrypa* dormitzeri' from Slite limestones around Klintehamn: these specimens were not available for study. The illustrations of Hede suggest that they

may belong to an undescribed species of *Hirciniscia*. If this is correct, *Hirciniscia* also occurs on Gotland. The species *Atrypa verna* (Barrande, 1879), and *Terebratula megaera* (Barrande, 1847), assigned by Havlíček (1961) to *Hirciniscia*, are re-assigned here to *Septatrypa*, based on the rib variations seen in Gotland. The subgenus appears to occur first in latest Llandovery time in the Urals and Siberia, with possibly the last surviving into the Early Devonian in the Canadian Arctic.

Species tentatively assigned.

Hirciniscia asiatica Rong in Wan 1978b, Sichuan, S China, ?late Llandovery (see Rong and Yang, 1981).

?*Atrypa dormitzeri* Barrande 1879, Dlouha Hora, Prague Basin, Kopanina Fm., Ludlow.

Hirciniscia hebes Havlíček 1961, Kozle, Beroun, Prague Basin, Liten beds, Wenlock.

?*Idiospira kuntakhina* Lopushinskaya 1976, Kuntakakh River, Siberian Platform, late Llandovery.

Hirciniscia serva latiplicata Mizens 1981, W slopes Urals, Sergi riverbank, Araslan beds, Ludlow.

?*Idiospira menneri* Beznosova 1985, Asdak River, N Urals, Yarenei Formation, late Llandovery.

Hirciniscia (?) *posthircina* Tyazheva 1972, Ufa River, W slope S Urals, lower Syan beds, Lochkovian.

Hirciniscia rhynchonelliformis Havlíček and Plodowski 1974, Berounka River, Prague Basin, middle Liten beds, Wenlock.

Terebratula sappho Barrande 1847, Zadní Kopanina, Prague Basin, lower Kopanina Fm., early Ludlow.

Atrypa serva Barrande 1879, Dlouha Hora, Prague Basin, Kopanina Limestones, Ludlow.

?*Linguopugnoides stelcki* Perry, 1984, Yukon, Canada, 62–68 m below top of Delorme Fm., Pragian–?Emsian.

Superfamily Glassioidea Schuchert and Levene, 1929

Family Glassiidae Schuchert and Levene, 1929

Subfamily Glassiinae Schuchert and Levene, 1929

Diagnosis (see also Copper, 2002b). Small to medium, smooth, biconvex, commonly ligate shells; thick walled; sturdy hinge socket plates, solid teeth usually reinforced by exposed or buried dental plates; dental cavities in later taxa; jugal processes terminated by small to large jugal plates; spiralia medially directed, fewer than 7 whorls, barrel-shaped, scooped towards jugal processes.

Range. ?Telychian, Wenlock–Frasnian.

Glassia Davidson, 1881

[= *Cryptatrypa* Siehl 1962, p. 196, type, *Terebratula philomela* Barrande, 1847, p. 387]

Type species. *Glassia elongata* Davidson 1881b [subsequent designation Copper, 1996c, p. 221, vide Copper, 2001c]. By original designation of Davidson (1881), the type species was *Atrypa obovata* Sowerby 1839. There is only a single specimen in the original Sowerby 'obovata' collection; it could not be serially sectioned. A number of externally very similar specimens of the same size and shape, identified as '*Glassia obovata*' by previous collectors, located in the Natural History Museum, London, and the Sedgwick Museum, Cambridge, were sectioned (see under *Lissatrypa obovata* herein). These specimens are all internally undoubtedly assignable to the genus *Lissatrypa* Twenhofel 1914, and lack the medially oriented spiralia that Davidson revealed for *Glassia elongata*. Davidson (1881b) selected the type without examination internally, but used the internal structure of the species, *Glassia elongata*, to determine the striking medial orientation of the spiralia. In order to preserve taxonomic stability, as the genera *Glassia* and *Lissatrypa* belong to two different superfamilies, the type species of *Glassia* was changed to *G. elongata* [Copper, 2001c]. The alternative would be to change all the present species of *Lissatrypa* to the genus *Glassia*, to select a new genus name for what has

been called *Glassia*, to change the descriptions of the two subfamilies, and to select a new name for the superfamily Glassioidea and the family replacing the Glassiidae. Since this would create taxonomic confusion, this alternative was abandoned.

Range and distribution. Western Europe, Urals, central Asia: ?Telychian, Wenlock–Pridoli. In Great Britain and Gotland, *Glassia* appears to occur only in rocks of Wenlock age. Nikiforova (1961) illustrated a middle Llandovery species, '*Glassia*' *mogoktaensis* from Siberia, which was shown to have medially directed spiralia as seen in true *Glassia*. This may represent a new genus, as it has a sharp fold with a few ribs along the commissure, but its distinctive spiralia may mark it as the ancestor of Wenlock *Glassia*. The middle Ashgill genus *Xysila* from Anticosti Island (Copper, 1995) has medially directed spiralia and a jugum connecting these, and it is the probable ancestor of the Glassiidae. Jugum or jugal processes and the medially directed spiralia were not shown for the Siberian species, so the exact affinities of *Glassia mogoktaensis* are unknown. *Glassia* in both Britain and Gotland occur in a deeper water facies, probably equivalent to BA-4 or BA-5 in the Llandovery equivalents. It is usually absent in communities which have colonial corals, calcareous algae, or photosynthetic calcimicrobes, and was therefore probably situated below the photic zone (as indicated also for the Prague Basin, by Turek, 1983).

Diagnosis. As in Copper (1986). It should be added that a median septum dividing the muscle field appears to be prominent in both valves, but is longer in the pedicle valve where it caps a wider central muscle platform.

Remarks. Although internally very different from *Lissatrypa* with dorsally directed spiralia, *Glassia* externally is also smooth and more or less biconvex, and almost a homeomorph. The two genera have often been confused in the literature, and only serial sectioning makes differences un-

mistakable. *Glossia* may be differentiated externally from *Lissatrypa* by a more ventribiconvex, globose shell which is usually pinched by a medial sulcus on each valve (bisulcation is not always present). The beak is incurved, area in anacline position and foramen usually transapical in this Silurian genus. The anterior and lateral commissure commonly are formed into a lip. *Lissatrypa* is rounded in outline and biconvex, with a rectimarginate or plicate commissure. Internally, *Glossia* lacks the pedicle callist-collar complex of *Lissatrypa*, possesses teeth with dental cavities, and has a very different hinge-plate structure that incorporates a prominently incised notothyrial cavity separating the inner socket plates. *Glossia* is, of course, highly distinct in its medially directed, barrel-shaped spiralia, while *Lissatrypa* has dorsal, conical spiralia. *Glossia* has frequently been reported from rocks of late Llandovery and younger age in the U.K., commonly as members of the '*Glossia*' community. Specimens of Llandovery age reported as *Glossia*, e.g., those from the Hughley Shale in England (*Glossia minuta* herein) and Wenlock shales and limestones, are usually referable to *Lissatrypa*. Similarly, common museum specimens from the Much Wenlock Limestone at Dudley, reported as *Glossia obovata*, belong to the genus *Lissatrypa*. This may mean that *Glossia* probably disappeared from Gotland and the U.K. near the end of Wenlock time, but persisted elsewhere into the Late Silurian.

Havlíček (1990) regarded the Silurian genus *Cryptatrypa* Siehl 1962 as distinct from Silurian *Glossia* on the basis of the lack of an area and deltidial plates, but the area is usually obscured by beak incurvature, and this trait is not evident. Siehl (1962) did not find the medially directed spiralia diagnostic of his genus *Cryptatrypa*, but the hinge plate and tooth structure is identical to that of *Glossia*. Silurian *Glossia* appear to lack a distinct area only since the beak is incurved and tends to obscure the area, but a small area is indeed present, and deltidial plates are usually minute or barely visible. The type species of *Cryptatrypa*, *C. philomela* Barrande 1847, is from the upper Motol Formation, of late Wenlock age. This is identical to the occurrence of *Glossia* in the Wenlock shales of England and Gotland. Havlíček (1990) was also neither able to find the spiralia or jugal plates nor identify the distinctive hinge plate, which would have helped to settle this problem. *Cryptatrypa* has pedicle cavities, teeth, and hinge plates like those of *Glossia*. I thus regard the two genera as synonymous, until the spiralia of *C. philomela* are shown to be different. Median septa in both valves are insignificant to absent in the Devonian genus *Peratos* (Copper, 1986). The loss of septa in Devonian taxa (they have not been described for the Lower Devonian genus *Karbous* Havlíček) may mark another evolutionary trend in addition to enlargement of the dental cavities, development of a prominent dental plate, increase in size of the area, and progression towards an orthocline beak. Once internal spiralia are confirmed, there should be other new species of the genus discovered elsewhere outside Europe and the Altai.

Species tentatively assigned [in addition to those listed in Copper, 1986, and the type species].

Glossia djanvika n. sp., western Gotland, Mulde beds, Wenlock.

?*Terebratula ephemera* Barrande 1847, Dlauha Hora, Prague Basin, Kopanina Fm., Ludlow.

Atrypa laevigata Kunth 1865, Tempelhof, Berlin [glacial erratic], 'Graptolithengestein', ?Ludlow.

Atrypa gutta Haupt 1878, erratics North Germany, 'Graptolithenkalke', Ludlow.

Terebratula philomela Barrande 1847, Prague Basin, upper Motol Fm., Wenlock.

Cryptatrypa praecordata Kulkov 1974, NW Altai, Chinetin Horizon, late Llandovery.

The species *Meristella* (?) *cordata* Kulkov 1963 and *Cryptatrypa pseudosecuris* Kulkov 1970, from the Pragian/Emsian Malobachat beds of NE Salair, can probably be assigned to the genus *Karbous* (Havlíček, 1985), if they have medially directed spiralia.

Glossia elongata Davidson, 1881

Pl. 29B, figs. a-i; Figs. 93-95

1881b *Glossia elongata* Davidson, p. 148-149, pl. 5, figs. 3, 3a-c, 4 (and figure p. 149).

1882 *Glossia elongata*, Davidson, pl. 7, figs. 9-10.

Type locality and stratum. '... railway cut between Farley Dingle and Tickwood', Britain (Davidson, 1881a, p. 103). No more precise locality or horizon is cited in the original description of the species, but this is about 3 km NNE of Much Wenlock, at Wenlock Edge. Davidson and Maw (1881, p. 103) extracted the shells from the Tickwood shales by sieving and washing, and mentioned also 'the deep road cutting near the railway bridge' and 'the side of a small stream flowing down the east end of Benthall Edge'. No fresh outcrop has apparently been available since the 1970s. The type stratum is the upper Coalbrookdale Formation (Sheinwoodian-Homerian), Farley Member [or Tickwood beds in the older literature, e.g., Davidson, 1881a]. This roughly spans the high *nassa* Zone, and is of late Wenlock age, preceding the deposition of the Much Wenlock Limestone at Wenlock Edge (Cocks, 1978). Cocks (1978) selected as lectotype B5493, the original illustrated by Davidson on pl. 5, fig. 3 (1881b), from the Coalbrookdale Formation of 'Wenlock Edge, Salop', presumably the same locality designated as the locus typicus by Davidson. Other specimens were also available from Wenlock shales at Scarf (Severn River) and Dudley. The Tickwood beds represent a deeper, distal shelf or slope facies.

Diagnosis. Relatively small, elongate to oval, biconvex; widths averaging 5 mm, depths 3 mm; narrow apical angle; swept-back shoulder line; lacking a sinus on both valves; straight jugal processes; spiralia with 3-4 whorls.

Description. Shells are very small; averaging 5 mm wide, ca. 3 mm deep; well-rounded outline; somewhat elongate, lengths exceeding width; maximum length 9.6 mm; beak small, protruding; anacline area; minute transapical foramen; narrow, weakly indented hinge line; hinge angles 90°-110°; anterior commissure rectimarginate, lacking any narrow distinct grooves or bisulcation; concentric growth lines only faintly defined. Internally, small, narrow dental cavities only posteriorly, closing up anteriorly; muscle scars deep; median ventral septum long, continuous from apex to mid-shell; teeth

Fig. 93. *Glossia elongata* Davidson, 1881. Scatter diagrams for width, length, depth, and frequency curves for width, depth, based on Davidson's specimens 'Tickwood', upper Wenlock Shales, late Wenlock. Sketch outlines show camera lucida drawings of typical small and larger specimens, detail of ventral apex.

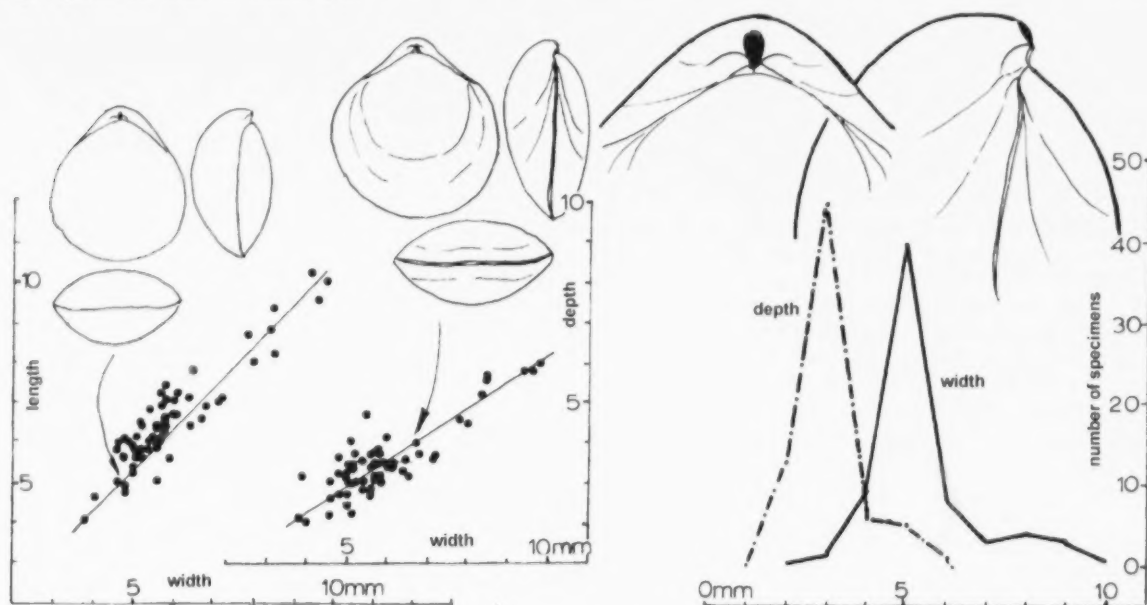
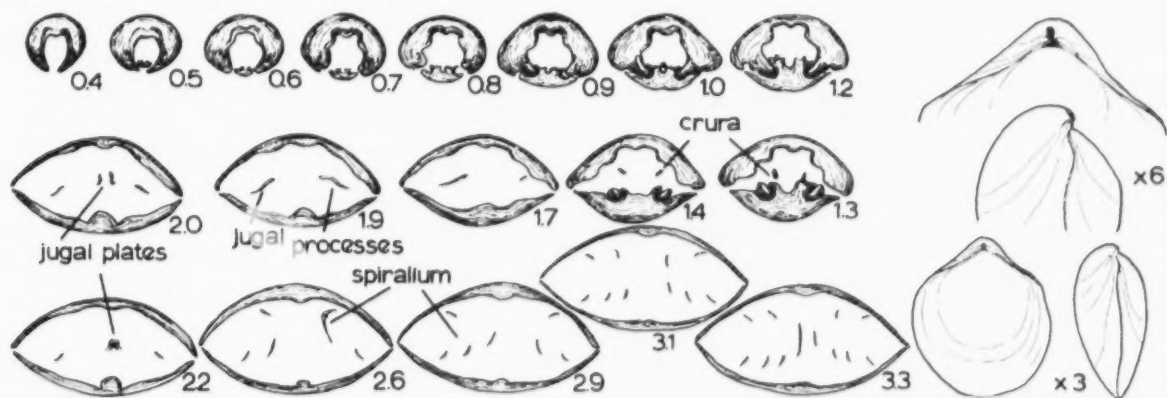


Fig. 94. *Glossia elongata* Davidson, 1881. Serial sections of specimen Br34856 from type locality Tickwood, upper Wenlock Shales, late Wenlock; camera lucida drawing of adult shell, all $\times 5$.



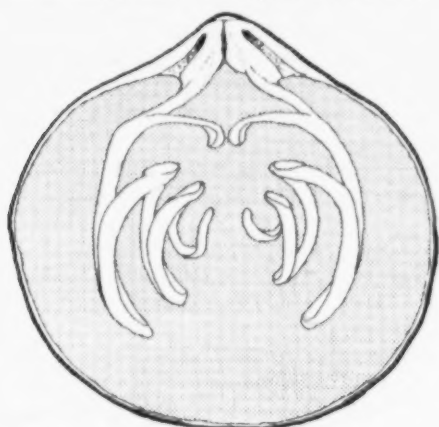
short, dorsomedially directed, lacking lateral lobes; small cardinal pit closing as narrow slit, flanked by two pointed inner socket ridges from hinge plate; hinge plates thick, solid; crural bases small, ventrolaterally directed; delicate crura, unfeathered; jugal processes nearly straight, tilted ventromedially; hook-shaped jugal plates touching centrally; spirillum with 3–4 whorls, barrel-shaped, medially directed.

Remarks. Davidson (1881b) illustrated the internal structure of '*Glossia obovata*', as developed from acid-etched specimens prepared by Norman Glass. As seen from museum remnants, this specimen is actually *Glossia elongata*, and not *Lissatrypa obovata*, which has led partially to the long-term confusion surrounding the internal structure of the genus. As seen from Davidson's sketch (1881b, p. 149), and corroborated here by serial sections, the postero-medial parts

of each whorl are directed in a funnel-like fashion towards the jugal processes, which are erroneously shown as being fused into a jugum in Davidson (1881b). The type species of *Glossia* is distinguishable from *Glossia djauvika* and *G. laevigata* Kunth (1865) in its smaller size (50% smaller), its longer than wide shell, its lack of a double sulcus at the commissure and its narrower apical angle.

Materials. Total 413 specimens from the Tickwood beds, Tickwood beds, locus typicus 'railway bridge, between Farley Dingle and Tickwood', BB34922 [19], B34856 [59], BB34857 [30], BB34924 [10], GSM61122–24 [3], GSM10388–09 [10], GSM103811–19 [8], GSM103820–29 [10], GSM103833–43 [5]; 'Tickwood and neighbourhood Salop', BB5495 [20; Davidson coll., BB68828]; N end of Scarf, Severn River, Lower Wenlock Shale B1598 [218, Maw coll.]; Wenlock

Fig. 95. *Glassia elongata* Davidson 1881. Reconstruction of spiralia of based on section Fig. 94, Br34856, upper Wenlock Shales, late Wenlock. Note medially directed spiralia and scooped, barrel-shaped structure of spiral whorls; $\times 10$.

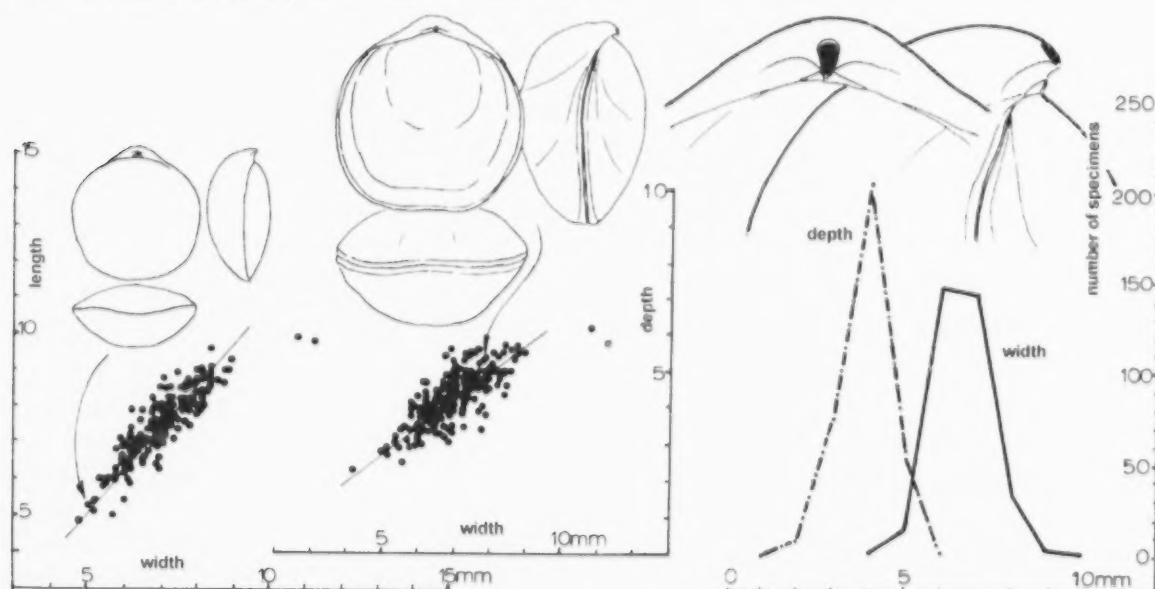


Shale, Tickwood, A26443-55 [13]; 'Dudley, upper Wenlock Shale', BB54816 [8]. The species was not found in Gotland, where it should occur in the upper Slite beds, unless specimens from Svarvare are counted in this assemblage: these specimens are larger and appear to belong to the same series as specimens from the Mulde Formation.

Glassia djauvika n. sp.
Pl. 29C, figs. a-m; Figs. 96, 97

?1878 *Atrypa gutta* Haupt, p. 67, pl. 2, figs. 6a-c.

Fig. 96. *Glassia djauvika* n. sp. Statistical evaluation of width, length, depth for specimens from Djupviksvägen 1, collected from a single nest along a bedding plane surface, Mulde Brick Clay Member, Mulde Marl, middle Wenlock. Camera lucida sketches show morphology of a neanic and adult specimen, detail of ventral umbo.



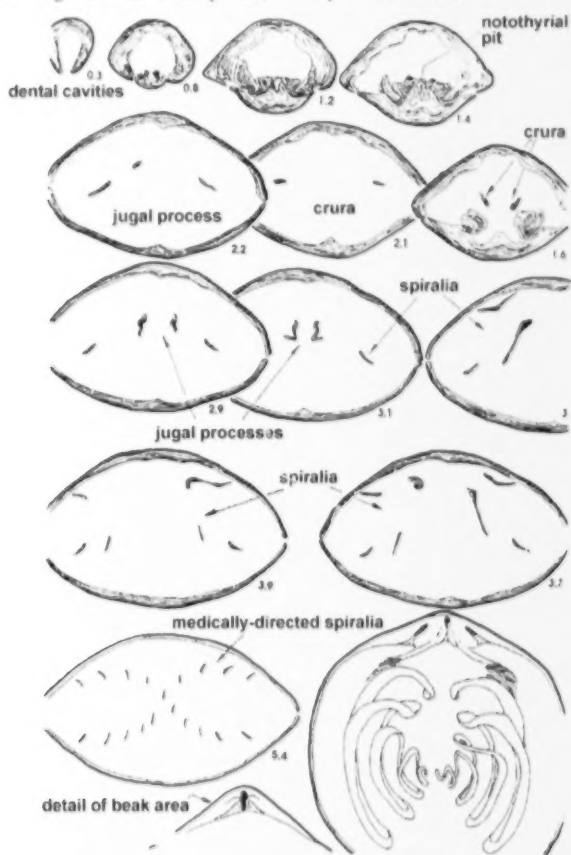
1899 *Atrypa obovata* Sowerby 1839, Venyukov, pl. 1, fig. 21.

?1970 *Glassia obovata* (Sowerby), Rubel, 38-39, pl. 16, figs. 7-25.

1986 *Glassia elongata* Davidson 1881, Copper, pl. 74, figs. 22-31, pl. 75, figs. 2, 7

Type locality and stratum. **Djupviksvägen 1**, Mulde Marl, *nassa* Zone, about 1 m of fossiliferous shale exposed about 300 m SW of Hajstade, 61 Visby SO 55730:41660 (= SW44), an excavated ditch locality on the north side of the road Bopparve-Djauvik, exposed in 1974 (about 4 km SW of Fröjel). This level is probably the middle Mulde Marl stratigraphically above Djupvik 2 (Laufeld, 1974), lower Homerian, late Wenlock. Co-occurring brachiopods are mostly small shells: larger *Gotatrypa muldea*, *Leptaena*, and *Meristina* are missing at this site. Several old collections with specimens morphologically almost the same as this species have been identified as occurring within the 'upper Slite beds', e.g., south and east of Klintehamn (the localities Svarvare, Sickling, and Odvalds; see Munthe, Hede, and Lundqvist, 1927, map sheet and p. 31 citation of '*Glassia compressa*'). This raises the possibility that these *Glassia*-bearing beds within the 'Slite Formation', which lie nearly along strike, are either of Mulde age (and thus misidentified on maps) or that the species ranges down through Slite strata into the *lundgreni* Zone. Munthe, Hede, and Lundqvist (1927, p. 31, Kartbladet Klintehamn) appear to have identified this species within the upper Slite as '*Glassia compressa*'. Munthe, Hede, and von Post (1927, p. 21, Kartbladet Hemse) identified '*Glassia obovata*' in the Mulde Marl as co-occurring with *Gothogaptus nassa*; thus the type stratum of *Glassia djauvika* can be assigned to at least the *nassa* Zone. The Mulde facies is a distal shelf, deeper water facies, probably below normal wave base.

Fig. 97. *Glossia djaavika* n. sp. Serial sections and reconstruction of the spiralia, specimen from Djupviksvägen 1, Mulde Brick Clay Member, Mulde Marl, middle Wenlock; note especially sections of whorls at 3.4–3.9 mm ($\times 5$), detail of beak showing small deltidial plates, transapical foramen, $\times 6.5$.



Diagnosis. Biconvex; distinctly bisulcate–rectimarginate; somewhat squared anterior commissure; averaging 6–7 mm wide, 4 mm deep; slightly longer than wide; strongly incurved beak; perforated apical foramen.

Description. Rounded to slightly squared anterior outline; ventral umbo protruding about 1 mm; vv slightly more convex than dv; rounded umbo; moderately wide apical angle averaging 100° – 110° ; weak shoulder incurvature; beak protruding; area anacline to nearly hypercline, protruding away from dorsal umbo; foramen transapical in adults, apical in shells <4 mm wide; minute, triangular deltidial plates, obscured by beak; anterior commissure rectimarginate to bisulcate, usually with distinct, inbent lip; shell smooth, with no significant growth interruptions. Internally, minute dental cavities at apex only, flanked by thin, nearly straight dental plates, lined by thick shell; teeth short, solid distally, at 45° to commissural plane, dorsomedially directed, with weak lateral stubs; dv with narrow, triangular groove bisecting thick hinge plate, covered by plate extending from inner socket ridge and crural bases; inner socket ridges massive, stubby; crural bases minute, rounded apically; short crura,

partly fibrous distally; jugal processes curved, ventromedial in location, terminating in vertical small jugal plates; spiralia barrel-shaped, directed medially, with posterior first whorl scooped, forming funnel or trough directed posteriorly.

Remarks. The serial sections indicate that the development of spiralia is rather different in *Glossia* than in other atrypoids: this is evident in serial sections taken at 3.4, 3.7, and 3.9 mm, anterior to the jugal processes (see Figs. 96, 97). The postero-medial portion of each whorl, especially seen in the first whorl, forms a scoop-like structure directed towards the jugal processes, unknown in other atrypoids. This suggests that the spiralia acted as a funnel towards the jugal processes, and that nutrients were thus directed towards the mouth (with the assumption that the mouth, and the digestive tract, were supported by the jugal processes). The base of each spiralia, and the coiled lophophore, therefore functioned to channel food to the middle of the shell cavity, and that waste must have been disposed towards the anterior commissure. Thus the unique morphology of the spiralia in *Glossia* provides a major clue as to the direction of inhalant feeding currents from the sides of the shell towards the exhalant centre of the anterior commissure. *Glossia djaavika* is very similar in some respects to *G. philomela* (Barrande, 1847), especially in the orientation and shape of the beak and foramen, but the latter is more ventribiconvex and less elongate, having a weak dorsal fold.

Glossia djaavika is nearly twice the size of *G. elongata*, more rounded and squared in outline, and with a double sulcus in adult shells. *Glossia laevigata* (Kunth, 1865), from glacial erratics near Berlin, is about the same size, but more rounded and ventribiconvex [see also illustrations of glacially derived Gotland species in Heidenhain (1869), Roemer (1885), and Gagel (1890)]. The Kunth specimens appear to be lost, and cannot be directly compared, and the species *laevigata* remains a nomen oblitum, as it has not been used in 135 years. Kunth (1865) figured the distinctive medially directed spiralia about 16 years before the genus was first described by Davidson (see first description and reconstructions of internal structure of *Glossia* in Copper, 1986). Another species described from German glacial erratics by Haupt in 1878, *Atrypa gutta*, is very similar in shape and also has a small anterior double crease (i.e., bisulcate condition); again, no material is available for comparison and this name also remains a nomen oblitum. Shells from the Lerberget locality on Stora Karlsö are somewhat smaller (ca. 20% smaller) than those from western Gotland, but this may be a local variety. The precise horizon from which the Lerberget shells were collected is unknown, as a visit there in 1990 did not turn up new specimens. *Glossia* on Gotland occur exclusively in shaly facies of the Mulde type, but only in select horizons and then abundantly enough to form 80% of the bottom community, as at the type locality, almost forming a *Glossia* community. This suggests highly localized environments on muddy substrates, and nested clusters: other fauna includes rare *Atrypa* and small *Meristina*. Rare, small favositid corals, but no bryozoans, stromatoporoids, or calcareous algae were found, suggesting deeper water depths, probably below the photic zone. The Mulde Marl faunas from the Mulde brickyard, and more recently, Gannarve, lack *Glossia*; here they may have been crowded out by other

brachiopod species. Old collections have abundant small specimens: in these collections the species ranges down into the upper Slite beds, and perhaps up into the lower Hemse beds, extending its range from the *lundgreni* through *nils-soni* zones.

Material. About 1650 specimens from the Mulde and upper Slite beds, with a single specimen from the west facies of the lower Hemse beds at Snoder 1. *Mulde Marl*: type locality, **Djupviksvägen 1**, ditch excavation N of Bopparve-Djauvik road [SW44: 422 shells]; **Sudervik 2**, beach locality about 1.5 km S of Kronvald, 51420:38050, probably the same horizon as the type locality [SW45: 41]; **Kronvall-**

snaset, Eksta sn., Br45444-540 [97]; **Djupvik**, Eksta sn. [Gamla coll.: 204]; Gannarve, Frojel sn. Br45064-429 [365]; **Svarvare 1** (this locality cited as Slite beds in Laufeld, 1974, but atrypid fauna suggests this is Mulde Marl), Klinte sn., Br120731-51 [21]; **Odvalds 1**, Klinte sn., ?Mulde Marl Br131145 [1]; **Kanalen SO om Klintehamn**, Klinte sn., ?Mulde Marl, Br120720-30 [11]; **800 m SV om Säckling**, Klinte sn., Br108441-50 [10]. ?*Slite beds*: **Stora Karlsö, Lerberget**, Br44905-52 [48], Br120613-54 [45]; Br61140 [1]; **Valbytte 1**, Sanda sn., Br123391-401 [11]; **Kanalen i Smittebergs aker**, Klintehamn, Klinte sn., Br47854-63 [10], Br46686-96 [11]; **Eksta** sn., Br45437-43 [7]; ?*Hemse beds*: **Snoder 1**, Slite sn., Br134551 [1].

Conclusions

1. Reasonably accurate correlations, using the atrypoid brachiopods (as checked against known graptolite ranges) may be carried out over a distance of more than 1500 km from the British Silurian siliciclastic ramp section to the Gotland and Estonia carbonate and reefal shelf. The areas carry a broadly similar atrypoid fauna, despite regional facies differences, although the Gotland reef-bearing section is considerably more diverse. Similar faunas also occur in neighbouring classic areas of Podolia (Ukraine) and the Prague Basin, suggesting faunal communication.
2. The internal structure of more than 45 species is clarified, most for the first time, and the generic assignment of species, especially type species of classic genera, e.g., *Atrypa*, *Gotatrypa*, *Oglupes*, *Reticulatrypa*, *Eospinatrypa*, *Spirigerina*, and *Atrypina*, is more accurately defined. This has enabled more accurate subfamily assignment, and clarification of atrypoid evolutionary trends and lineages, also for the first time for the Middle and Late Silurian.
3. A first attempt is made to assign the northwest European atrypoids to specific facies belts in relation to shallow on-shore and distal offshore tropical carbonate platform settings. These do not necessarily match standard benthic assemblage (BA) water depth assignments, which appear more appropriate to ramp than shelf settings. Atrypid families or genera appear to have played mixed roles in either reefal or non-reefal settings. Some started off in one setting, only to change preferences later; although *Spirigerina* was a reef dweller in Wenlock time, this role

was not occupied by its ancestor, *Eospirigerina* in the Hirnantian or Llandovery. *Atrypaidea* generally lived in a more restricted, shoreward level bottom community, but occasionally preferred a reef habitat. *Eospinatrypa* started off in ooid shoals, only to move to deeper water muddy bottoms in the Devonian.

4. The late Llandovery through Ludlow was a period of atrypoid radiation in tropical low latitude settings, with many subfamilies common to the Devonian, and many early character traits used for later Devonian refinement of evolutionary trends, appearing for the first time. For example, the Wenlock marked the first radiation of many ribbed plectatrypines, atrypines, spirigerines, and spinatrypines, and the evolution of morphological features such as elaborate frills, spines, and micro-ornament.
5. The constant shifts of Middle and Late Silurian atrypoid brachiopod communities through the Anglo-Welsh Embayment and Baltic Basin, the lack of distinctive and recognizable persistent associations of major brachiopod orders and families (e.g., atrypids with pentamerids, athyridids, rhynchonellids, or spiriferids, or even other phyla such as corals and stromatoporoids), and the repeated additions of evolving new species and genera, and similar losses of existing taxa up section, suggested that the terms 'coordinated stasis' as well as 'Ecologic Evolutionary Units' are highly unsuitable for such constantly evolving communities. In addition, most of the changes within communities (e.g., the percentage combinations of various brachiopod orders within communities or assemblages) appear to be unpredictable, random, stochastic, or fortuitous.



References

- Aaloe, A.O., and Nestor, H. 1977. Biohermal facies in the Juuru Stage (Lower Llandoveryan) in northwest Estonia. p. 71-88. *In* Facies and Fauna of the Baltic Silurian. Edited by D. Kaljo. Akademiya Nauk, Tallinn. 286 pp.
- Abbott, B.M. 1976. Origin and evolution of bioherms in the Wenlock Limestones (Silurian) of Shropshire, England. *Bulletin American Association of Petroleum Geologists*, **60**: 2117-2127.
- Aldridge, R. 1975. The stratigraphical distribution of conodonts in the British Silurian. *Journal of the Geological Society (London)*, **131**: 607-618.
- Aldridge, R., Jeppsson, L., and Dörning, K.J. 1993. Early Silurian oceanic episodes and events. *Journal of the Geological Society (London)*, **150**: 501-513.
- Alekseeva, R.E. 1966a. K voprosu o stroenii ruchnogo apparata roda *Atrypa* Dalman [On questions of the structure of the brachial apparatus in the genus *Atrypa* Dalman]. *Paleontologicheskii Zhurnal*, **3**: 66-73.
- Alekseeva, R.E. 1966b. O rode *Spirigerina* Orbnig [On the genus *Spirigerina* Orbnig]. *Paleontologicheskii Zhurnal*, **4**: 63-68.
- Alekseeva, R.E. 1962. Devonskie atripidy Kuznetskogo i Minusinskogo basseinov i vostochnogo sklona severnogo Urala [Devonian Atrypids of the Kuznetsk and Minusinsk Basins and the Eastern Slopes of the Northern Urals]. Akademiya Nauk, Sibirskoe Otdelenie, Izdatelstvo Nauk, Moskva. 192 pp.
- Alekseeva, R.E. 1968. O sistematicheskoi znachenii shleifov i gli atripid [On the systematic significance of frills in the atrypid group]. *Trudy Institut Geologii Geofiziki, Sibirskoe Otdelenie*, **112**: 109-111.
- Alekseeva, R.E. 1970. Otryad Atrypida [Order Atrypida]. p. 104-141. *In* Stratigrafiya i brachiopody nizhnego Devona severo-vostochnogo Salaira [Stratigraphy and Brachiopods of the Lower Devonian of Northeastern Salair]. Edited by R.E. Alekseeva, R.T. Gratsianova, E.A. Elkin, and N.P. Kulkov. Trudy Institut Geologii Geofiziki, Sibirskoe Otdelenie, **72**: 1-190.
- Alekseeva, R.E., and Kulkov, N.P. 1970. *Septatrypa* ? *gratsianovae* sp. nov., p. 137-138. *In* Stratigrafiya i brachiopody nizhnego Devona severo-vostochnogo Salaira [Stratigraphy and Brachiopods of the Lower Devonian of Northeastern Salair]. Edited by R.E. Alekseeva, R.T. Gratsianova, E.A. Elkin, and N.P. Kulkov. Trudy Institut Geologii Geofiziki, Sibirskoe Otdelenie, **72**: 1-190.
- Alexander, F.E.S. 1949. Revision of the brachiopod species *Anomia reticularis* Linnaeus, genoelectotype of *Atrypa* Dalman. *Quarterly Journal of the Geological Society, London*, **104**: 207-220.
- Alikhova, T.N. 1954. Gotlandii Brachiopody [Gotlandian brachiopods]. p. 35-43. *In* Polevoi atlas kharakternykh kompleksov fauny otlozhenii Ordovika i Gotlandiya yuzhnoi chasti Litovskoi SSSR [Field Atlas of Characteristic Faunal Complexes of the Ordovician and Gotlandian Strata in the Southern Part of Lithuanian USSR]. Edited by T.N. Alikhova, E.A. Balashova, and Z.G. Balashov. Trudy VSEGEI, Leningrad. 99 pp.
- Amsden, T.W. 1949. Two new genera of brachiopods from the Henryhouse Formation (Silurian) of Oklahoma. *Journal of the Washington Academy of Sciences*, **39**(6): 202-203.
- Amsden, T.W. 1951. Brachiopods of the Henryhouse Formation (Silurian) of Oklahoma. *Journal of Paleontology*, **25**: 69-96.
- Amsden, T.W. 1958a. Haragan articulate brachiopods. *Oklahoma Geological Survey Bulletin*, **78**: 7-144.
- Amsden, T.W. 1958b. Supplement to the Henryhouse brachiopods. *Oklahoma Geological Survey Bulletin*, **78**: 145-158.
- Amsden, T.W. 1968. Articulate brachiopods of the St. Clair Limestone (Silurian), Arkansas, and the Clarita Formation (Silurian), Oklahoma. *Memoirs Paleontological Society*, **1**: 1-117.
- Amsden, T.W. 1978. Articulate brachiopods of the Quarry Mountain Formation (Silurian), eastern Oklahoma. *Oklahoma Geological Survey Bulletin*, **125**: 1-75.
- Andasheva, N.A. 1980. Novyi vid Siluriiskikh atripid vostochnogo Kazakhstana [New species of Silurian atrypid from eastern Kazakhstan]. *Novye Vidy Drevnikh Rastenii Bespozvonochnykh SSSR* [New species of ancient plants and invertebrates USSR], **5**: 80-81.
- Angelin, N.P., and Lindström, G. 1880. *Fragmenta silurica e dono Caroli Henrici Wegelin*. Samson and Wallin, Holmia. 61 pp.
- Antoshkina, A.I., and Beznosova, T.M. 1988. Novye dannye po stratigrafii Venlovskikh otlozhenii bolshezemelskoi tundry [New data on the stratigraphy of Wenlock strata in the Bolshzemel tundra]. *Byulleten Geologii*, **6**: 32-39.
- Azmy, K., Verzer, J., Bassett, M.G., and Copper, P. 1998. Oxygen and carbon isotopic composition of Silurian brachiopods: implications for coeval seawater and glaciations. *Geological Society of America Bulletin*, **110**: 1499-1512.
- Baily, W.H. 1875. *Figures of Characteristic British Fossils with Descriptive Remarks*. Van Voorst, London. 126 pp.
- Barrande, J. 1847. Ueber die Brachiopoden der silurischen Schichten von Böhmen. *Naturwissenschaftlichen Abhandlungen Wilhelm Haidinger*, **1**: 357-475, pl. 14-22.
- Barrande, J. 1879. *Système Silurien du Centre de la Bohême. Première Partie. Recherches Paléontologiques*, **5**, Classe des Mollusques, Ordre des Brachiopodes. Chez Vauteur, Prague. 226 pp., 153 pl.
- Bassett, M.G. 1974. Review of the stratigraphy of the Wenlock Series in the Welsh Borderland and south Wales. *Palaeontology*, **17**: 745-777.
- Bassett, M.G. 1976. A critique of diachronism, community distribution and correlation at the Wenlock-Ludlow boundary. *Lethaia*, **9**: 207-218.
- Bassett, M.G. 1979. Brachiopods. p. 185-206. *In* Lower Wenlock Faunal and Floral Dynamics — Vattenfallet Section, Gotland. Edited by V. Jaanusson, S. Laufeld, and R. Skoglund. Sveriges Geologiska Undersökning, **C762**: 1-294.
- Bassett, M.G. 1986. Silurian stratigraphy and facies development in Scandinavia. p. 283-292. *In* The Caledonide Orogen — Scandinavia and Related Areas. Edited by D.G. Gee and B.A. Sturt. John Wiley & Sons, Inc., New York.
- Bassett, M.G. 1989. The Wenlock Series in the Wenlock area. p. 51-73. *In* A Global Standard for the Silurian System. Edited by C.H. Holland and M.G. Bassett. National Museum Wales, Geological Series, **9**: 1-325.
- Bassett, M.G. 1990. Life strategies of Silurian brachiopods. *Special Papers in Palaeontology*, **32**: 237-263.
- Bassett, M.G., and Cocks, L.R.M. 1974. A review of Silurian articulate brachiopods of Gotland. *Fossils Strata*, **3**: 1-56.
- Bassett, M.G., Cocks, L.R.M., Holland, C.H., Rickards, R.B., and Warren, P.T. 1975. The type Wenlock Series. *Report Institute Geological Sciences*, **75/13**: 1-19.
- Bassett, M.G., Kaljo, D., and Teller, L. 1989. The Baltic region. p. 158-170. *In* A Global Standard for the Silurian System. Edited by C.H. Holland and M.G. Bassett. National Museum Wales, Geological Series, **9**: 1-325.
- Batchelor, R.A., and Jeppsson, L. 1994. Late Llandovery benthites from Gotland, Sweden, as chemostratigraphic markers. *Journal of the Geological Society (London)*, **152**: 741-746.
- Bergman, C.F. 1980. Macrofossils of the Wenlockian Slite Siltstone of Gotland. *Geologiska Föreningens Förhandlingar*, **102**: 13-25.
- Bergman, C.F. 1989. Silurian paulinitid polychaetes from Gotland. *Fossils Strata*, **25**: 1-128.

- Bergström, S.M., Huff, W.D., Kolata, D.R., and Kaljo, D. 1992. Silurian K-bentonites in the Iapetus region: a preliminary event-stratigraphic and tectonomagmatic assessment. *Geologiska Föreningens Förhandlingar*, **114**: 327–334.
- Beznosova, T.M. 1977. Novye silurijskie brachiopody Pai-Khoya i podnyatiya Chernova. [New Silurian brachiopods from Pai-Khoy and the Chernova Rise]. *Ezhgodnik Institut Geologii Komi Filiala AN SSR*, **1976**: 34–39.
- Beznosova, T.M. 1985. Novye rannesilurijskie brachiopody Evropeiskogo severo-vostoka SSSR [New Early Silurian brachiopods from the European northeastern USSR]. *Trudy Instituta Geologii, Komii Filial, Akademii Nauk SSR*, **54**: 3–16.
- Beznosova, T.M. 1994. Biostratigrafiya i brachiopody Silura Evropeiskogo Severo-Vostoka Rossii [Silurian Biostratigraphy and Brachiopods, European Northeastern Russia]. *Russkaya Akademiya Nauk, Moskva*, 128 pp.
- Beznosova, T.M., and Mizens, L.I. 1980. Lissatrypidae Grebenskoi Gorizonta (Przhidoli) Pechorskogo Urala [Lissatrypidae from the Greben Horizon (Pridoli), Pechora Urals]. *Paleontologiya i biostratigrafiya Srednego Paleozoya Urala [Akademiya Nauk, Uralskii Nauchnyi Tsentr, Sverdlovsk]*, **1980**: 55–72.
- Bickert, T., Pätzold, J., Samtleben, C., and Munneke, A. 1997. Paleoenvironmental changes in the Silurian indicated by stable isotopes in brachiopod shells from Gotland, Sweden. *Geochimica Cosmochimica Acta*, **61**: 2717–2730.
- Biernat, G., and Godefroid, J. 1992. Redescription des genres *Septatrypa* Kozłowski 1929, et *Dubaria* Termier, 1936. *Bulletin Institut Royal Sciences Naturelles Belgique, Sciences Terre*, **62**: 43–60.
- Billings, E. 1862. New species of fossils from different parts of the Lower, Middle, and Upper Silurian rocks of Canada. *Palaeozoic fossils, Geological Survey of Canada, Montreal*, **1**(4): 96–168.
- Billings, E. 1866. Catalogue of the Silurian Fossils of the Island of Anticosti, with Descriptions of Some New Genera and Species. *Geological Survey of Canada, Montreal*, 93 pp.
- Blainville, H.M. Ducrotay de. 1825, 1827. *Manuel de malacologie et de conchyologie*, Levrault, Paris, 664 pp., 95 pl. (Text and pl. 1–55, 1825; pl. 56–95, 1827.)
- Borisovskiy, M.A. 1955a. Silurijskie (Venlovskie) brachiopody iz Karagandinskoi Oblasti [Silurian (Wenlock) brachiopods from the Karagandinsk region]. *Materialy Vsesoyuznogo Nauchno-issledovatel'skogo Geologicheskogo Instituta (VSEGEI), Paleontologia Stratigrafiya*, **3**: 1–107.
- Borisovskiy, M.A. 1955b. Stratigrafiya i brachiopody Silurijskikh otlozhenii raiona Khrebt Chingiz [Stratigraphy and brachiopods of Silurian strata from the Chingiz Mountain region]. *Materialy Vsesoyuznogo Nauchno-issledovatel'skogo Geologicheskogo Instituta (VSEGEI), Paleontologia Stratigrafiya*, **5**: 1–105.
- Boucot, A.J. 1964. A new genus of Silurian atrypacean brachiopod. *Quadrangle Map Series Maine Geological Survey*, **2**: 1–105.
- Boucot, A.J. 1975. *Evolution and Extinction Rate Controls*. Elsevier Science B.V., Amsterdam, 427 pp.
- Boucot, A.J., and Amsden, T.W. 1958. New genera of brachiopods, p. 159–170. *In* *Stratigraphy and Paleontology of the Hunton Group in the Arbuckle Mountain Region, Oklahoma*. Edited by T.W. Amsden and A.J. Boucot. *Bulletin Oklahoma Geological Survey*, **78**: 1–199.
- Boucot, A.J., and Johnson, J.G. 1964a. Brachiopods of the Ede Quartzite (Lower Llandovery) of Norderön, Jämtland. *Bulletin Geological Institute University Uppsala*, **42**: 1–11.
- Boucot, A.J., and Johnson, J.G. 1964b. On some atrypoid, retzioid, and athyroid Brachiopoda. *Journal of Paleontology*, **38**: 805–822.
- Boucot, A.J., and Johnson, J.G. 1967. Silurian and Upper Ordovician atrypids of the genera *Plectatrypa* and *Spirigerina*. *Norsk Geologisk Tidsskrift*, **47**: 79–101.
- Boucot, A.J., Johnson, J.G., and Staton, R.D. 1965. Order Spiriferida. p. 633–648. *In* *Treatise on Invertebrate Paleontology*, Brachiopoda. Edited by R.C. Moore. Geological Society of America and University of Kansas Press, Lawrence, KS. **H2**: 524–927.
- Boucot, A.J., Johnson, J.G., and Zhang, N. 1988. Silurian (Wenlockian) brachiopods from southeastern California. *Palaeontographica*, **A201**: 103–127.
- Bowen, Z.P. 1966. Intraspecific variation in the brachial cardinalia of *Atrypa reticularis*. *Journal of Paleontology*, **40**: 1017–1022.
- Brazauskas, A., and Musteikis, P. 1991. Brachiopod and conodont distribution at the Wenlock–Ludlow boundary of Lithuania. *Toimetised Eesti Teaduste Akadeemia*, **40**: 61–68.
- Breivel, I.A., and Breivel, M.G. 1977. Brachiopods, p. 52–105. *In* *Biostratigrafiya i fauna Rannego Devona vostochnogo sklona Urala [Biostratigraphy and Fauna of the Early Devonian of the Eastern Slopes of the Urals]*. Edited by M.G. Breivel. *Ministerstvo Geologii Uralskoe Territorialnoe Geologicheskoe Upravlenie, Moskva*, 245 pp.
- Breivel, I.A., and Breivel, M.G. 1988. Biostratigrafiya i brachiopody Silura Vostochnogo Sklona Urala [Biostratigraphy and Brachiopods of the Silurian of the Eastern Slopes of the Urals]. *Ministerstvo Geologii SSSR, Uralskoe Proizvodstvennoe Geologicheskoe Otdelenie, Moskva*, 204 pp.
- Brett, C.E., and Baird, G.C. 1995. Coordinated stasis and evolutionary ecology of Silurian to Middle Devonian faunas in the Appalachian basin, p. 285–315. *In* *New Approaches to Speciation in the Fossil Record*. Edited by D.H. Erwin and R.K. Anstey. Columbia University Press, New York.
- Brett, C.E., Boucot, A.J., and Jones, B. 1993. Absolute depths of Silurian benthic assemblages, Lethaia. **26**: 25–40.
- Brown, T. 1849. *Illustrations of the Fossil Conchology of Great Britain and Ireland with Descriptions and Localities of all the Species*. Smith Elder and Co., London, 274 pp.
- Brunton, C.H.C., Cocks, L.R.M., and Dance, S.P. 1967. Brachiopods in the Linnaean collection. *Proceedings Linnaean Society, London*, **178**: 161–183.
- Bublikhenko, N.L. 1927. Die Brachiopodenfauna des unteren Palaeozoicum aus der Umgegend des Dorfes Sara-Tschumysch aus den Kohlenbassin von Kusnetsk. *Bulletin Comité Géologique*, **46**(8): 979–1008.
- Buch, L. von. 1835. Über Terebrateln, mit einem Versuch, sie zu classificiren und zu beschreiben. *Physikalische Abhandlungen der Königl. Akademie für Wissenschaften aus den Jahre 1833*, **1835**: 21–144, pl. 1–3. Berlin. [According to J. Ewald, J. Roth, and W. Dames. 1882. *Zeitschrift Deutschen Geologischen Gesellschaft*, **32**: vi. This lecture was given by von Eichwald in 1833, but published in 1835, although the date of publication on the volume is shown as 1834.]
- Buch, L. von. 1840. Beiträge zur Bestimmung der Gebirgsformationen in Russland. *Archiv für Mineralogie, Geognosie, Bergbau und Hüttenkunde*. Reimer Verlag, Berlin, **15**: 3–128, pl. 1–3. [Republished under J. Ewald, J. Roth, and W. Dames. 1885. *Leopold von Buch's gesammelte Schriften*, Berlin **4**(2): 566–656, pl. 32–35.]
- Calef, C.E., and Hancock, N.H. 1974. Wenlock and Ludlow marine communities. *Palaeontology*, **17**: 779–810.
- Calner, M. 1999a. Stratigraphy, facies development, and depositional dynamics of the late Wenlock Fröjel Formation, Gotland, Sweden. *Geologiska Föreningens Förhandlingar*, **121**: 13–24.
- Calner, M. 1999b. Comments to the mid-late Homerian sea-level curve. *Lund Publications Geology*, **144**: 1.
- Calner, M. 2000. Stratigraphy and facies of Middle Silurian epicontinental carbonate platform deposits of Gotland (Sweden). *Lund Publications Geology*, **150**: 1–18.
- Calner, M. 2002. A lowstand epikarstic intertidal flat from the Middle Silurian of Gotland, Sweden. *Sedimentary Geology*, **148**: 389–404.

- Calner, M., and Jeppsson, L. 1999. Emersion and subaerial exposure in the Silurian of Gotland—response to a mid-Homerian glaciation. *Geologiska Föreningens Förhandlingar*, **121**: p. 78.
- Calner, M., and Jeppsson, L. 2002. Middle Silurian carbonate depositional environments and conodont stratigraphy from Gotland, Sweden. *Geological Magazine*, **139**: 123–131.
- Calner, M., and Säll, E. 1999. Transgressive oolites onlapping a Silurian rocky shoreline unconformity, Gotland, Sweden. *Geologiska Föreningens Förhandlingar*, **121**: 99–100.
- Calner, M., Sandström, O., and Mötus, M.A. 2000. Significance of a halysitid-heliolitid mud-facies autobiostrome from the Middle Silurian of Gotland, Sweden. *Palaios*, **15**: 511–523.
- Cherns, L. 1982. Palaeokarst, tidal erosion surfaces and stromatolites in the Silurian Eke Formation of Gotland, Sweden. *Sedimentology*, **29**: 119–183.
- Cherns, L. 1983. The Hemse–Eke boundary: facies relationships in the Ludlow series of Gotland, Sweden. *Sveriges Geologiska Undersökning*, **C800**: 1–45.
- Cherns, L. 1988. Faunal and facies dynamics in the Upper Silurian of the Anglo-Welsh Basin. *Palaeontology*, **31**: 451–502.
- Chernyshev, T. 1885. Die Fauna des untern Devon am West-Abhänge des Urals. *Trudy Geologicheskii Komitet*, **3**: 1–107.
- Chernyshev, T. 1893. Die Fauna des untern Devon am Ostabhänge des Urals. *Trudy Geologicheskii Komitet*, **4**: 1–221.
- Chiang, K.K. 1972. A late Wenlockian brachiopod fauna from the Amabel Formation of Ontario. *Journal of Paleontology*, **46**: 15–30.
- Cocks, L.R.M. 1967. Depth patterns in Silurian marine communities. *Marine Geology*, **5**: 37–382.
- Cocks, L.R.M. 1978. A review of British Lower Palaeozoic brachiopods including a synoptic revision of Davidson's monograph. *Palaeontographical Society Monographs*, **131**: 1–256.
- Cocks, L.R.M., and Baarli, B.G. 1982. The late Llandovery brachiopods from the Oslo region. *Paleontological Contributions University Oslo*, **278**: 78–89.
- Cocks, L.R.M., and Fortey, R.A. 1988. Lower Palaeozoic facies and fauna around Gondwana. *Geological Society Special Publication*, **37**: 183–200.
- Cocks, L.R.M., Holland, C.H., Rickards, R.B., and Strachan, I. 1971. Silurian. *Journal Geological Society*, **127**: 103–136.
- Cocks, L.R.M., Holland, C.H., and Rickards, R.B. 1992. A revised correlation of Silurian rocks in the British Isles. *Geological Society London, Special Report*, **21**: 1–32.
- Copper, P. 1965. Devonian Atrypids of Northwestern Europe. Ph. D. thesis. Imperial College of Science and Technology, London. 460 pp.
- Copper, P. 1966. Ecological distribution of Devonian atrypid brachiopods. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **2**: 254–66.
- Copper, P. 1973a. The type species of *Lissatrypa* (Silurian Brachiopoda). *Journal of Paleontology*, **47**: 70–76.
- Copper, P. 1973b. New Siluro-Devonian atrypoid brachiopods. *Journal of Paleontology*, **47**: 484–500.
- Copper, P. 1974. Structure and development of early Paleozoic reefs. *Proceedings Second International Coral Reef Symposium*, Panama, **2**: 365–386.
- Copper, P. 1976. The cyanophyte *Wetheredella* in Ordovician reef and off-reef sediments. *Lethaia*, **9**: 273–81.
- Copper, P. 1977a. *Zygospira* and some related Ordovician and Silurian atrypoid brachiopods. *Palaeontology*, **20**: 295–335.
- Copper, P. 1977b. The Late Silurian brachiopod genus *Atrypoides*. *Geologiska Föreningens Förhandlingar*, **99**: 10–26.
- Copper, P. 1982. Early Silurian atrypoids from Manitoulin Island and Bruce Peninsula, Ontario. *Journal of Paleontology*, **56**: 680–702.
- Copper, P. 1986. Evolution of the earliest smooth spire-bearing atrypoids (Brachiopoda: Lissatrypidae, Ordovician-Silurian). *Palaeontology*, **29**: 827–866.
- Copper, P. 1994. Ancient reef ecosystem expansion and collapse. *Coral Reefs*, **13**: 3–11.
- Copper, P. 1995. Five new genera of Late Ordovician–Early Silurian brachiopods from Anticosti island, eastern Canada. *Journal of Paleontology*, **69**: 846–862.
- Copper, P. 1996a. *Davidsonia* and *Rugodavidsonia* (new genus), cryptic Devonian atrypid brachiopods from Europe and South China. *Journal of Paleontology*, **70**: 588–602.
- Copper, P. 1996b. New and revised genera of late Wenlock–Ludlow atrypids (Silurian Brachiopoda) from Gotland, Sweden, and the United Kingdom. *Journal of Paleontology*, **70**: 913–923.
- Copper, P. 1996c. Atrypida, p. 81–85. In P. Copper and R. Gourvennee, Evolution of the spire-bearing brachiopods (Ordovician–Jurassic), p. 81–88. *Edited by P. Copper and J. Jin, Brachiopods*, Balkema Press, Rotterdam. 373 pp.
- Copper, P. 1997a. Articulate brachiopod shellbeds: Silurian examples from Anticosti, eastern Canada. *Geobios Monographies Spéciales*, **20**: 133–148.
- Copper, P. 1997b. Reefs and carbonate productivity: Cambrian through Devonian, p. 1623–1630. *Edited by H.A. Lessios and I.G. Macintyre, Proceedings of the 8th International Coral Reef Symposium*, Panama, **1**: 1–1049.
- Copper, P. 2001a. Radiations and extinctions of atrypid brachiopods: Ordovician–Devonian, p. 201–211. In *Brachiopods Past and Present*, *Edited by C.H.C. Branton, L.R.M. Cocks, and S.L. Long*, Systematics Association Special Volume Series, **63**: 1–441.
- Copper, P. 2001b. Originations and extinctions in brachiopods, p. 249–261. In *Brachiopods Ancient and Modern*, *Edited by S.J. Carlson and M.R. Sandy*, Paleontological Society Papers, **7**: 1–261.
- Copper, P. 2001c. *Glassia* (Davidson 1881) (Brachiopoda): proposed designation of *G. elongata* Davidson, 1881 as the type species. *Bulletin Zoological Nomenclature*, **58**(4): 1–3.
- Copper, P. 2002a. Silurian and Devonian reefs: 80 millions years of global greenhouse between two ice ages, p. 181–238. In *Phanerozoic Reef Patterns*, *Edited by W. Kiessling, E. Flügel, and J. Golonka*, Society Economic Paleontologists Mineralogists (SEPM) Special Publication, **72**: 1–776.
- Copper, P. 2002b. Atrypida, p. 1376–1474. In *Brachiopoda, Treatise on Invertebrate Paleontology*, *Edited by A. Williams, C.H.C. Branton, and S.J. Carlson*, Geological Society of America and University of Kansas Press, Lawrence (revised), **H4**: 1–1688.
- Copper, P., and Branton, F.R. 1991. A global review of Silurian reefs. *Special Papers in Paleontology*, **44**: 225–260.
- Copper, P., and Chen, Y. 1995. *Invertina*, a new genus of atrypoid brachiopod from South China. *Journal of Paleontology*, **69**: 251–256.
- Copper, P., and Gourvennee, R. 1996. Evolution of the spire-bearing brachiopods (Ordovician–Jurassic), p. 81–88. In *Brachiopods*, *Edited by P. Copper and J.S. Jin*, Balkema Press, Rotterdam. 373 pp.
- Copper, P., and Jin, J.S. (Editors). 1996. *Brachiopods*, Balkema Press, Rotterdam. 373 pp.
- Copper, P., and Long, D.G.F. 1998. Sedimentology and paleontology of the Late Ordovician through Early Silurian shallow water carbonates and reefs of Anticosti Island, Québec, p. 55–95. In *Sedimentology and Paleontology of the Early Ordovician Through Early Silurian Shallow Water Carbonates of the Mingan Islands National Park and Anticosti Islands, Québec*, Field Trip Guidebook, *Edited by A. Desrochers, P. Copper, and D.G.F. Long*, Annual Meeting Geological Association of Canada, Québec, **B8**: 1–97.
- Copper, P., and Racheboeuf, P.R. 1985. Devonian atrypoid brachiopods from the Armorican Massif, northwestern France. *Palaeontographica*, **187A**: 58–104.
- Copper, P., and Rubel, M. 1977. *Atrypoides saaremaensis* n. sp. *Geologiska Föreningens Förhandlingar*, **99**: 23–24.

- Copper, P., Hünicken, M., and Benedetto, J.L. 1988. Revision of the Silurian brachiopod *Australina* from the Malvinokaffric faunal province. *Journal of Paleontology*, **62**: 531–538.
- Corfield, R.M., Siveter, D.J., Cartledge, J.E., and McKerrow, W.S. 1992. Carbon isotope excursion near the Wenlock–Ludlow boundary (Silurian) in the Anglo-Welsh area. *Geology*, **20**: 371–374.
- Crosfield, M.C., and Johnson, M.S. 1914. A study of "ballstone" and associated beds in the Wenlock Limestone. *Proceedings Geological Association*, **25**: 193–224.
- Curtis, M.L.K., Lawson, J.D., Squirell, H.C., Tucker, E.V., and Walmsley, V.G. 1967. The Silurian inliers of the south-eastern Welsh Borderland. *Geological Association Guidebooks*, **5**: 1–32.
- Dalman, J.W. 1828. Uppställning och beskrifning af de i Sverige funne terebratuliter. *Konglige Svenska Vetenskaps Akademiens Handlingar*, **1827**: 85–155.
- Davidson, T. 1848. Mémoire sur les brachiopodes du système Silurien supérieur d'Angleterre. *Bulletin Société Géologique France*, **5**: 309–338 [with pl. 3].
- Davidson, T. 1853. On the classification of the Brachiopoda. *British fossil Brachiopoda*. *Palaeontographical Society Monographs*, **1(3)**: 1–136.
- Davidson, T. 1866. A monograph of the British fossil Brachiopoda, The Silurian Brachiopoda. *Palaeontographical Society Monographs*, **7(3)**: 1–88.
- Davidson, T. 1867. A monograph of the British fossil Brachiopoda, The Silurian Brachiopoda. *Palaeontographical Society Monographs*, **7(3)**: 89–168.
- Davidson, T. 1868. The Silurian Brachiopoda of the Pentland Hills. *Transactions Geological Society Glasgow, Palaeontological Series*, **1**: 1–24.
- Davidson, T. 1869. A monograph of the British fossil Brachiopoda, The Silurian Brachiopoda. *Palaeontographical Society Monographs*, **7(3)**: 169–248.
- Davidson, T. 1871. A monograph of the British fossil Brachiopoda, The Silurian Brachiopoda. *Palaeontographical Society Monographs*, **7(4)**: 249–397.
- Davidson, T. 1881a. On genera and species of spiral-bearing Brachiopoda, from specimens developed by the Rev. Norman Glass: with notes on the results obtained by Mr. George Maw from extensive washings of the Wenlock and Ludlow Shales of Shropshire. *Geological Magazine*, **8**: 1–12.
- Davidson, T. 1881b. Descriptions of new Upper Silurian Brachiopoda from Shropshire. *Geological Magazine*, **8**: 145–156.
- Davidson, T. 1882. A monograph of the British fossil Brachiopoda, Supplement to the British Silurian Brachiopoda. *Palaeontographical Society Monographs, Supplement*, **5(1)**: 1–134.
- Davidson, T. 1883. A monograph of the British fossil Brachiopoda, Supplement to the British Silurian Brachiopoda. *Palaeontographical Society Monographs, Supplement*, **5(2)**: 135–242.
- Davidson, T., and Maw, G. 1881. Notes on the physical character and thickness of the Upper Silurian rocks of Shropshire, with the Brachiopoda they contain grouped in geological horizons. *Geological Magazine*, **8**: 100–109.
- Defrance, J.L.M. 1827. Dictionnaire des sciences naturelles. Levraut, Strasbourg and Paris, **50**: 293–295. [Atlas prepared by H.M.D. Blainville, 118 pl., various annual dates from 1816 to 1830.]
- Deshayes, G.P. 1797, 1827, 1832. *Encyclopédie méthodique*. Agassé, Paris. [Pl. 190–286 by E. Bruguère in 1797; text by G.P. Deshayes, p. 145–1152, in 1817, 1832.]
- Doyle, E.N., Harper, D.A.T., and Parkes, M.A. 1990. The Tonalee fauna: a deep-water shelly assemblage from the Llandovery rocks of the west of Ireland. *Irish Journal Earth Sciences*, **10**: 127–143.
- Dun, W.S. 1904. Notes on some new species of Palaeozoic Brachiopoda from New South Wales. *Records Geological Survey New South Wales*, **7(4)**: 318–329.
- Earp, J.R., and Hains, B.A. 1971. The Welsh Borderland [3rd ed.]. *British Regional Geology*, Institute Geological Sciences, London. 118 pp.
- Edinger, E.N., Copper, P., Risk, M.J., and Atmojo, W. 2002. Oceanography and reefs of recent and Paleozoic tropical epeiric seas. *Facies*, **47**: 127–150.
- Eichwald, E. von. 1829. *Zoologia specialis*. St. Petersburg, Golike, **1**: 1–314.
- Eichwald, E. von. 1840. Ueber das Silurische Schichtensystem in Esthland. *Zeitschrift Natur Heilkunde*, St. Petersburg, **1(2)**: 1–210.
- Eichwald, E. von. 1846. Einige Bemerkungen zur geognosie Scandinaviens und der westlichen Provinzen Russlands. *Bulletin Naturalistes, Moscou*, **19**: 1–156.
- Eichwald, E. von. 1854. Die Grauwackenschichten von Liev- und Esthland, Königsberg. 111 pp.
- Eichwald, E. von. 1860. *Lehæa Rossica ou paléontologie de la Russie*. Golike, St Petersburg [in French], **1(2)**: 681–1657. [Also 1855 German edition Schweizerbart'sche Buchhandlung, Stuttgart; 1861 edition Golike, St. Petersburg, in Russian.]
- Fang, R. 1974. *Atrypella inflata* n.sp. p. 394. *Brachiopoda*. p. 285–480. In *Atlas of Fossils from Yunnan*. Edited by R. Fang and X. Chu. Yunnan Institute Geological Sciences, Kunming. 560 pp.
- Fang, R. 1985. Brachiopoda. p. 52–69. In *The Middle Silurian and Early Devonian Stratigraphy and Palaeontology in Qujing District, Yunnan*. Edited by R. Fang, N. Jiang, J. Fan, R. Cao, and D. Li. Yunnan Institute Geological Sciences, Kunming. 171 pp.
- Foerste, A.F. 1890. Notes on Clinton group fossils, with special reference to the collections from Indiana, Tennessee and Georgia. *Proceedings Boston Society Natural History*, **24**: 263–355.
- Franke, W. 1999. Tectonic and plate tectonic units at the north Gondwana margin: evidence from the central European Variscides. *Abhandlungen Geologischen Bundesanstalt*, **54**: 7–13.
- Fredholm, D. 1988a. Vertebrates in the Ludlovian Hemse Beds of Gotland, Sweden. *Geologiska Föreningens Förhandlingar*, **110**: 157–179.
- Fredholm, D. 1988b. Vertebrate biostratigraphy of the Ludlovian Hemse Beds of Gotland, Sweden. *Geologiska Föreningens Förhandlingar*, **110**: 237–253.
- Frykman, P. 1985. Subaerial exposure and cement stratigraphy of a Silurian bioherm in the Klinteberg Beds, Gotland, Sweden. *Geologiska Föreningens Förhandlingar*, **107**: 77–88.
- Frykman, P. 1986. Diagenesis of Silurian bioherms in the Klinteberg Formation, Gotland, Sweden. In *Reef Diagenesis*. Edited by J.H. Schroeder and B. Purser. Springer, Heidelberg. pp. 399–423.
- Frykman, P. 1989. Carbonate ramp facies of the Klinteberg Formation Wenlock–Ludlow transition on Gotland, Sweden. *Sveriges Geologiska Undersökning*, **C820**: 1–79.
- Fu, L. 1982. Brachiopoda. p. 95–179. In *Paleontological Atlas of Northwest China, Shaanxi-Gansu-Ningxia*, 1, Precambrian and Early Paleozoic. Xian Institute Mineral Resources, Xian, 480 pp.
- Fu, L. 1985. Early Silurian brachiopods from Zhaohuajing, Tongxin County, Ningxia. *Bulletin Xian Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences*, **9**: 90–102.
- Fürsich, F.T., and Hurst, J.M. 1974. Environmental factors determining the distribution of brachiopods. *Palaeontology*, **17**: 879–900.
- Gaertner, H.R. von. 1930. Silurische und tiefunterdevonische Trilobiten und Brachiopoden aus den Zentralkarnischen Alpen. *Jahrbuch Preussischen Geologischen Landesanstalt*, **51**: 188–252.
- Gägel, C. 1890. Die Brachiopoden der cambrischen und silurischen Geschiebe in Diluvium der Provinzen Ost- und Westpreußen. *Beiträge Naturkunde Preußen*, **6**: 1–79.
- Giebel, C.G. 1858. Die silurische Fauna des Unterharzes. *Ahandlungen Naturhistorische Verein Halle*, **1**: 263–332.

- Gill, T. 1871. Arrangement of the families of molluscs prepared for the Smithsonian Institution. Smithsonian Miscellaneous Collections, **227**: 1-49.
- Ginley, W. 1878. Notice of the discovery of the position of the crural processes in the genus *Atrypa*. Proceedings American Philosophical Society, **17**: 337-338.
- Godefroid, J. 1991. *Solitudinella hollardi* n. gen., n. sp., (Brachiopoda, Lissatrypidae) dans le Praguien du Maroc pré-saharien. Bulletin Institut Royal Sciences Naturelles Belgique, Sciences Terre, **61**: 107-121.
- Golonka, J. 2002. Plate-tectonic maps of the Phanerozoic. p. 21-75. In Phanerozoic Reef Patterns. Edited by W. Kiessling, E. Flügel, and J. Golonka. Society Economic Paleontologists Mineralogists (SEPM) Special Publication, **72**: 1-775.
- Grabau, A.W. 1925. Summary report on the faunas of the Xingtan Shale [western Hubei]. Geological Survey of China Bulletin, **7**: 77-85.
- Grabau, A.W. 1926. Silurian faunas of eastern Yunnan. Palaeontologica Sinica, **B3**: 1-86.
- Gratsianova, R.T. 1967. Brachiopody i stratigrafiya Nizhnego Devona Gomoego Alaya [Brachiopods and Stratigraphy of the Lower Devonian of the Altai Mountains]. Akademiya Nauk SSSR, Sibirskoi Otdelenie Institut Geologii Geofiziki, Novosibirsk. 160 pp.
- Grubbs, D.M. 1939. Fauna of the Niagaran nodules of the Chicago area. Journal of Paleontology, **13**: 543-560.
- Gruenewaldt, M. 1854. Ueber die Versteinerungen der silurische Kalke von Bogoslovsk. Mémoires Savants Etrangères, St. Petersburg, **7**: 571-620.
- Hadding, A. 1950. Silurian reefs of Gotland. Journal Geology, **58**: 402-409.
- Hall, J. 1852. Containing descriptions of the organic remains of the lower middle division of the New York System. Natural History New York, Palaeontology, Benthuyssen, Albany, **2**: 1-362.
- Hall, J. 1857. Descriptions of new species of fossils from the lower Helderberg, Oriskany Sandstone, upper Helderberg, Hamilton and Chemung groups. Annual Report New York State Cabinet Natural History, **10**: 41-186.
- Hall, J. 1859. Containing descriptions of the organic remains of the Lower Helderberg Group and the Oriskany Sandstone. Palaeontology of New York, Benthuyssen, Albany, **3**: 1-532. [Pl. 1-63.]
- Hall, J. 1867. Containing descriptions and figures of the fossil Brachiopoda of the upper Helderberg, Hamilton, and Chemung groups. Natural History of New York, Benthuyssen, Albany, **4**: 1-428. [Pl. 1-120, 1861.]
- Hall, J. 1879. The fauna of the Niagara group. Report New York State Museum Natural History, **28**: 98-203.
- Hall, J., and Clarke, J.M. 1892-1895. An Introduction to the Study of the Genera of Paleozoic Brachiopoda, New York State Survey, Albany. Part 1: 1-367, pl. 1-20 [1892]; Part 2: 1-317 [1893], 318-394 [1894], pl. 21-84 [1895]. [See part 2, p. xiv for explanation of publication dates.]
- Hamblin, R.J.O., Warwick, G.T., and White, D.E. 1978. Geological Handbook for the Wren's Nest National Nature Reserve. Nature Conservancy Council, London. 16 pp.
- Hancock, N.H.J., Hurst, J.M., and Fürsich, F.T. 1974. The depths inhabited by Silurian brachiopod communities. Journal Geological Society London, **130**: 151-156.
- Hardie, W.G. 1971. Wren's Nest Hill, Dudley. In The Area Around Birmingham. Edited by W.G. Hardie et al. Geological Association Guides, **1**: 7-12.
- Harland, W.B., Armstrong, R.L., Cox, A.V., Craig, L.E., Smith, A.G., and Smith, D.G. 1989. A Geologic Time Scale 1989. Cambridge University Press, Cambridge. 263 pp.
- Harper, C.W. 1969. Rib branching patterns in the brachiopod *Atrypa reticularis* from the Silurian of Gotland, Sweden. Journal of Paleontology, **43**: 183-188.
- Haswell, G.C. 1865. On the Silurian Formations of the Pentland Hills. Nimmo, Edinburgh. 47 pp.
- Haupt, K. 1878. Die Fauna des Graptolithengesteines. Ein Beitrag zur Kenntniss der silurischen Sedimentärgeschiebe der norddeutschen Tiefebene. Neues Lausitzisches Magazin, **54**: 29-113.
- Havlíček, V. 1960. Bericht über die Ergebnisse der Revision der böhmischen altpaläozoischen Rhynchonelloidea. Vestník Ústředního Ústavu Geologického, **35**: 241-244.
- Havlíček, V. 1961. Rhynchonelloidea des böhmischen älteren Paläozoikums (Brachiopoda). Rozpravy Ústředního Ústavu Geologického, **27**: 1-211.
- Havlíček, V. 1973. New brachiopod genera in the Devonian of Bohemia. Vestník Ústředního Ústavu Geologického, **48**: 337-340.
- Havlíček, V. 1984. *Lissatrypa* (Brachiopoda; Silurian, Lower Devonian) in Bohemia. Vestník Ústředního Ústavu Geologického, **59**: 217-225.
- Havlíček, V. 1985. *Karhouz* g. n. in Bohemia (Lissatrypidae, Brachiopoda; Devonian). Vestník Ústředního Ústavu Geologického, **60**: 235-239.
- Havlíček, V. 1987a. Lower Devonian and Eifelian Atrypacea (Brachiopoda) in central Bohemia. Sbornik Geologického Vedník, Paleontologia, **28**: 61-115.
- Havlíček, V. 1987b. New genera of Silurian brachiopods. Vestník Ústředního Ústavu Geologického, **62**: 239-243.
- Havlíček, V. 1990. Survey of articulate brachiopods. In Sedimentology, Benthic Communities, and Brachiopods in the Suchomasty (Dalejan) and Acanthopyge (Eifelian) Limestones of the Koneprusy Area (Czechoslovakia). Edited by V. Havlíček and Z. Kukal. Sbornik Geologických Ved Paleontologie, **31**: 128-205.
- Havlíček, V. 1991. Systematic paleontology. In Silurian Brachiopods and Communities in the Prague Basin (Czechoslovakia). Edited by V. Havlíček and V.L. Štorch. Rozpravy Ústředního Ústavu Geologického, **48**: 45-275.
- Havlíček, V. 1995. New data on the distribution of brachiopods in the Motol and lowest Kopanina formations (Wenlock, lower Ludlow, Prague Basin, Bohemia). Vestník Českého Geologického Ústavu, **70**: 47-64.
- Havlíček, V. 1998. Notes on the validity of several Silurian and Lower Devonian genera of Atrypida (Brachiopoda) in the Prague Basin, Czech Republic. Vestník Českého Geologického Ústavu, **73**: 51-54.
- Havlíček, V. 1999. Lochkovian brachiopods of the Prague Basin (Lower Devonian, Czech Republic). Vestník Českého Geologického Ústavu, **74**: 299-322.
- Havlíček, V., and Plodowski, G. 1974. Über die systematische Stellung der Gattung *Hireinisca* (Brachiopoda) aus dem böhmischen Ober-Silurium. Senckenbergiana Lethaea, **55**: 229-249.
- Havlíček, V., and Štorch, V.L. 1990. Silurian brachiopods and communities in the Prague Basin (Czechoslovakia). Rozpravy Ústředního Ústavu Geologického, **48**: 1-275.
- Hede, J.E. 1917. Fauna i kalksandstenens mårgliga bottenlager söder om Klintehamn på Gotland. Sveriges Geologiske Undersökning, **C281**: 1-32.
- Hede, J.E. 1921. Gotlands Silurstratigrafi. Sveriges Geologiska Undersökning, **C305**: 1-100.
- Hede, J.E. 1923. Contributions to the fossil fauna of Gotland. Sveriges Geologiska Undersökning, **C316**: 1-25.
- Hede, J.E. 1925-1940. Beskrivning av Gotlands Silurlager. Sveriges Geologiska Undersökning, **C331**: 13-30 [1925; see also Hede, J.E. In Kartbladet, Sveriges Geologiska Undersökning, (1927a), Aa160 Klintehamn, 12-48; (1927b), Aa164 Hemse, 15-56; (1928), Aa169 Slite, 13-65; (1929), Aa170 Katthammarsvik, 14-57; (1933), Aa171 Kappelshamn, (1936), Aa 180, Färö; (1940), Aa183 Visby-Lummelunda].
- Hede, J.E. 1960. The Silurian of Gotland. In The Lower Palaeozoic of Scania, The Silurian of Gotland, Guide to Excursions A22

- and C17. Guidebook XXI International Congress Norden, Copenhagen, 1960: 44–89.
- Hedström, H. 1910. The stratigraphy of the Silurian strata of the Visby district. *Geologiska Föreningens Förhandlingar*, **32**: 1455–1484.
- Hedström, H. 1923. Remarks on some fossils from the diamond boring of the Visby cement factory. *Sveriges Geologiska Undersökning*, **314**: 1–26.
- Heidenhain, F. 1869. Ueber Graptolithen führende Diluvial-Geschiebe der norddeutschen Ebene. *Zeitschrift Deutschen Geologischen Gesellschaft*, **21**: 143–181.
- Heritsch, F. 1930. Die obersilurische Fauna des Wiedatales im Harz. *Jahrbuch Preußischen Geologischen Landesanstalt*, **50**: 514–580.
- Hisinger, W. 1827. Gottland, geognostiskt beskrifvit. Öfversigt Konglige Vetenskap Akademiens Handlingar, **1826**: 311–337.
- Hisinger, W. 1828. Anteckningar i fysik och geognosie under resor uti sverige och norrige, **4**: 1–260.
- Hisinger, W. 1831a. Anteckningar i fysik och geognosie under resor uti sverige och norrige, **5**: 1–174.
- Hisinger, W. 1831b. Tableau des pétrifications de la Suède, rangées en ordre systematique. Norstedt, Stockholm. 43 pp.
- Hisinger, W. 1837. Lethaea suecica seu petrificata sueciae, iconibus et characteribus illustrata. Norstedt, Stockholm. 124 pp.
- Hoepen, E.C.N. van. 1910. De bouw van het Siluur van Gotland. Published Ph.D. thesis, Technische Hoogeschool, Delft. 161 pp.
- Holland, C.H. 1985. Series and stages of the Silurian System. *Episodes*, **8**: 101–103.
- Holtehdahl, O. 1924. On the rock formations of Novaya Zemlya with notes on the Paleozoic stratigraphy of other arctic lands. Report of the scientific results of the Norwegian Expedition to Novaya Zemlya 1921. Brøgers Boktrykkeri, Kristiania, **22**: 1–183.
- Hou, H.F., and Zhao, Z.M. 1976a. *Carinata crinata* Hou et Zhao (sp.nov.), p. 198. In *Paleontological Atlas of North China, Inner Mongolia, Paleozoic*. Geological Publishing House, Beijing. 502 pp.
- Hou, H.F., and Zhao, Z.M. 1976b. *Atrypella neimongolica* Hou et Zhao (sp.nov.), p. 202. In *Paleontological Atlas of North China, Inner Mongolia, Paleozoic*. Geological Publishing House, Beijing. 502 pp.
- Hurst, J.M. 1975a. The diachronism of the Wenlock Limestone, Lethaia, **8**: 301–314.
- Hurst, J.M. 1975b. Wenlock carbonate, level bottom, brachiopod-dominated communities from Wales and the Welsh Borderland. *Palaeogeography Palaeoclimatology Palaeoecology*, **17**: 227–255.
- Hurst, J.M. 1975c. Some observations on brachiopods and the level-bottom community ecology of Gotland. *Geologiska Föreningens Förhandlingar*, **97**: 250–264.
- Hurst, J.M., Hancock, N.H., and McKerrow, W.S. 1978. Wenlock stratigraphy and palaeogeography of Wales and the Welsh Borderland. *Proceedings Geologists' Association*, **89**: 197–226.
- Jaanusson, V. 1979. Stratigraphical and environmental background. In *Lower Wenlock Faunal and Floral Dynamics — Vattenfallet Section, Gotland*. Edited by V. Jaanusson, S. Laufeld, and R. Skoglund. *Sveriges Geologiska Undersökning*, **C762**: 11–38.
- Jaanusson, V. 1986. Locality designations in old collections from the Silurian of Gotland. Department Zoology, Riksmuseet, Stockholm. 19 pp. [Museum publication.]
- Jaanusson, V., Laufeld, S., and Skoglund, R. (Editors). 1979. Lower Wenlock faunal and floral dynamics — Vattenfallet section, Gotland. *Sveriges Geologiska Undersökning*, **C762**: 1–294.
- Jablonski, D., Sepkoski, J.J., Bottjer, D.J., and Sheehan, P.M. 1983. Onshore-offshore patterns in the evolution of Phanerozoic shelf communities. *Science*, **222**: 1123–1125.
- Jaeger, H. 1991. Neue Standard-Graptolithenzonenfolge nach der "großen Krise" an der Wenlock–Ludlow Grenze. *Neues Jahrbuch Geologie Paläontologie, Abhandlungen*, **182**: 103–154.
- Jeppsson, L. 1983. Silurian conodont faunas from Gotland. *Fossils Strata*, **15**: 121–144.
- Jeppsson, L. 1987. Lithological and conodont distributional evidence for episodes of anomalous oceanic conditions during the Silurian. In *Palaeobiology of Conodonts*. Edited by R. Aldridge. Ellis Horwood Ltd., Chichester. pp.129–145.
- Jeppsson, L. 1990. An oceanic model for lithological and faunal changes, tested on the Silurian record. *Journal of the Geological Society (London)*, **147**: 663–674.
- Jeppsson, L. 1997a. A new latest Telychian, Sheinwoodian and early Homerian (Early Silurian) standard conodont zonation. *Transactions Royal Society Edinburgh, Earth Sciences*, **88**: 91–114.
- Jeppsson, L. 1997b. Recognition of a probable secundo-primo event in the Early Silurian. *Lethaia*, **29**: 311–315.
- Jeppsson, L. 1997c. The anatomy of the mid-Early Silurian Ireviken event and a scenario for P-S events. In *Paleontological Events*. Edited by C.E. Brett and G.C. Baird. Columbia University Press, New York. pp. 451–492.
- Jeppsson, L. 1998. Silurian oceanic events: summary of general characteristics. p. 239–257. In *Silurian Cycles*. Edited by E. Landing and M.E. Johnson. New York State Museum Bulletin, **491**: 1–432.
- Jeppsson, L., and Calner, M. 2003. The Middle Silurian Mulde event and a scenario for secundo-secundo events. *Transactions Royal Society Edinburgh, Earth Sciences*, **93**: 1–22.
- Jeppsson, L., and Männik, P. 1993. High resolution correlations between Gotland and Estonia near the base of the Wenlock. *Terra Nova*, **5**: 345–358.
- Jeppsson, L., Viira, V., and Männik, P. 1994. Silurian conodont-based correlations between Gotland (Sweden) and Saaremaa (Estonia). *Geological Magazine*, **131**: 101–128.
- Jeppsson, L., Aldridge, R.J., and Dörning, K.J. 1995. Wenlock (Silurian) oceanic episodes and events. *Journal of the Geological Society (London)*, **152**: 487–498.
- Jin J.S., and Caldwell, W.G.E. 1990. *Rhytidorhachis*, a new Silurian rhynchonellid brachiopod from Gotland, Sweden, and the Hudson Bay Lowlands, Canada. *Bulletin Institute Royal Sciences Naturelles Belgique*, **60**: 29–41.
- Jin, J.S., and Copper, P. 2000. Late Ordovician and Early Silurian pentamerid brachiopods from Anticosti Island, Québec, Canada. *Palaeontographica Canadiana*, **18**: 1–140.
- Jin J.S., Caldwell, W.G.E., and Norford, B.S. 1993. Early Silurian brachiopods and biostratigraphy of the Hudson Bay Lowlands, Manitoba, Ontario and Quebec. *Geological Survey of Canada Bulletin*, **457**: 1–221.
- Johnson, J.G. 1967. *Toquimaella*, a new genus of karpinskiinid brachiopod. *Journal of Paleontology*, **41**: 874–880.
- Johnson, J.G. 1970. Great Basin Lower Devonian Brachiopoda. *Geological Society of America Memoirs*, **121**: 1–421.
- Johnson, J.G. 1973. Mid-Lochkovian brachiopods from the Windmill Limestone of Central Nevada. *Journal of Paleontology*, **47**: 1013–1030.
- Johnson, J.G., and Boucot, A.J. 1967. *Gracianella*, a new Late Silurian genus of atrypoid brachiopods. *Journal of Paleontology*, **41**: 868–873.
- Johnson, J.G., and Boucot, A.J. 1970. Brachiopods and age of the Tor Limestone of central Nevada. *Journal of Paleontology*, **44**: 265–269.
- Johnson, J.G., and Boucot, A.J. 1972. Origin and composition of the Carinatininae (Devonian Brachiopoda). *Journal of Paleontology*, **46**: 31–38.
- Johnson, J.G., Boucot, A.J., and Murphy, M.A. 1973. Pridolian and early Gedinnian age brachiopods from the Roberts Mountains Formation of central Nevada. *University California Publications Geological Sciences*, **100**: 1–75.
- Johnson, J.G., Boucot, A.J., and Murphy, M.A. 1976. Wenlockian and Ludlovian age brachiopods from the Roberts Mountains Formation of central Nevada. *University California Publications Geological Sciences*, **115**: 1–102.

- Jones, B. 1974. A biometrical analysis of *Atrypella foxi* n.sp. from the Canadian Arctic. *Journal of Paleontology*, **48**: 963–977.
- Jones, B. 1979a. *Atrypoides erebus* n.sp., from the Late Silurian of arctic Canada. *Journal of Paleontology*, **52**: 187–196.
- Jones, B. 1979b. *Atrypoides* zonation of the Upper Silurian Read Bay Formation of Somerset and Cornwallis Islands, Arctic Canada. *Canadian Journal of Earth Sciences*, **16**: 2204–2218.
- Jones, B. 1981. *Atrypoides* species from the Canadian arctic islands. *Canadian Journal of Earth Sciences*, **18**: 1539–1561.
- Jones, B. 1982. Paleobiology of the Upper Silurian brachiopod *Atrypoides*. *Journal of Paleontology*, **56**: 912–923.
- Jones, B. 1983. Analysis of growth patterns in brachiopods and its potential use for the identification of species. *Journal of Paleontology*, **57**: 662–685.
- Jones, B., and Hurst, J.M. 1984. Autecology and distribution of the Silurian brachiopod *Dubaria*. *Palaeontology*, **27**: 699–706.
- Jones, B., and Narbonne, G.M. 1984. Environmental controls on the distribution of *Atrypoides* species in Upper Silurian strata of arctic Canada. *Canadian Journal of Earth Sciences*, **21**: 131–144.
- Jones, B., and Packard, J. 1980. *Atrypoides polaris*: a new atrypoid brachiopod species from arctic Canada. *Journal of Paleontology*, **54**: 577–583.
- Jones, B., and Rong, J. 1982. Comparison of the Upper Silurian *Atrypoides* faunas of arctic Canada and southern China. *Journal of Paleontology*, **56**: 924–937.
- Jux, U. 1957. Die Riffe Gotlands und ihre angrenzenden Sedimentationsräume. *Stockholm Contributions Geology*, **1**: 41–89.
- Jux, U., and Steuber, T. 1992. C_{carb} - and C_{org} -Isotopenverhältnisse in der silurischen Schichtenfolge Gotlands als Hinweise auf Meeresspiegelschwankungen und Krustenbewegungen. *Neues Jahrbuch Geologie Paläontologie Monatshefte*, **1992**: 385–413.
- Kaljo, D. 1977. (Editor). Silurian Facies and Fauna of the Pribaltic. Akademiya Nauk Estonskoi SSR, Institut Geologii, Tallinn. 286 pp.
- Kaljo, D. 1996. Diachronous recovery patterns in Early Silurian corals, graptolites and acritarchs. In *Biotic Recovery from Mass Extinction Events*. Edited by M.B. Hart. Geological Society Special Publications, **102**: 127–133.
- Kaljo, D., Kiipli, T., and Martma, T. 1997. Carbon isotope event markers through the Wenlock Pridoli sequence at Ohesaare (Estonia) and Priekule (Latvia). *Palaeogeography Palaeoclimatology Palaeoecology*, **132**: 211–223.
- Kaljo, D., and Klaamann, E. (Editors). 1982a. Communities and Biozones in the Baltic Silurian. Akademiya Nauk Estonskoi SSR, Tallinn. 138 pp.
- Kaljo, D., and Klaamann, E. (Editors). 1982b. Ecostratigraphy of the East Baltic Silurian. Valgus Press, Tallinn. 109 pp.
- Kaljo, D., and Rubel, M. 1982. Relations of brachiopod communities to facial zones (Silurian, East Baltic). p. 11–35. In *Communities and Biozones in the Baltic Silurian*. Edited by D. Kaljo and E. Klaamann. Akademiya Nauk Estonskoi SSR, Tallinn. 138 pp.
- Kaljo, D., Nestor, H., and Einasto, R. 1991. Aspects of Silurian carbonate platform sedimentation. *Special Papers in Palaeontology*, **44**: 205–224.
- Kano, A. 1989. Deposition and paleoecology of an Upper Silurian stromatoporoid reef on southernmost Gotland. *Geological Journal*, **24**: 195–215.
- Kayser, E. 1878. Die Fauna der ältesten Devon-Ablagerungen des Harzes. *Abhandlungen Geologischen Spezialkarte Preußen Thüringer Staaten*, **2(4)**: 1–295.
- Kazanski, P. 1899. Materialien zur Kenntniss der Devon-Fauna des Urals. *Trudy Obshestvo Estestvo Imperialnogo Kazansk Universitet*, **34**: 1–50.
- Keeling, M., and Kershaw, S. 1994. Rocky shore environments in the Upper Silurian of Gotland, Sweden. *Geologiska Föreningens Föreläsningar*, **116**: 69–74.
- Kelus, A. 1939. Ramieninogi i koralowce dewonskie okolic Pelczy na Wolyniu [Devonian brachiopods and corals of the area of Pelczy in Volhynia]. *Biuletyn Panstwowy Instytut Geologiczny*, **8**: 1–51.
- Kershaw, S. 1981. Stromatoporoid growth form and taxonomy in a Silurian biostrome, Gotland, Sweden. *Journal of Paleontology*, **55**: 1284–1295.
- Kershaw, S. 1990. Stromatoporoid palaeobiology and taphonomy in a Silurian biostrome on Gotland, Sweden. *Palaeontology*, **33**: 681–705.
- Kershaw, S. 1993. Sedimentation control on growth of stromatoporoid reefs in the Silurian of Gotland, Sweden. *Journal of the Geological Society (London)*, **150**: 197–205.
- Kershaw, S., and Brunton, F.R. 1999. Paleozoic stromatoporoid taphonomy: ecologic and environmental significance. *Palaeogeography Palaeoclimatology Palaeoecology*, **149**: 313–328.
- Khalif, L.L. 1948. Fauna and stratigraphy of the Devonian strata of the Gorno Altai. *Izvestia Tomsk Politekhni Institut*, **65**: 1–464.
- Khodalevich, A.N. 1939. Verkhne-Silurijskie brachiopody vostochnogo sklona Urala [Upper Silurian brachiopods of the eastern slopes of the Urals]. *Trudy Uralskogo Geologicheskogo Upravleniya. Izdanie Uralgeoupravleniya, Sverdlovsk*. 135 pp.
- Khodalevich, A.N. 1951. Nizhnedevonskie i Eifelskie brachiopody Ivdelskogo i Serovskogo raionov Sverdlovskoi Oblasti [Lower Devonian and Eifelian brachiopods of the Ivdal and Serov regions of the Sverdlovsk District]. *Trudy Sverdlovskogo Gornoi Institut*, **18**: 1–169.
- Kiessling, W., Flügel, E., and Golonka, J. 2000. Fluctuations in the carbonate production of Phanerozoic reefs. *Geological Society London Special Publications*, **178**: 191–215.
- Kiessling, W., Flügel, E., and Golonka, J. (Editors). 2002. Phanerozoic reef patterns. *Society Economic Paleontologists Mineralogists (SEPM) Special Publication*, **72**: 1–775.
- King, W. 1846. Remarks on certain genera belonging to the class Palliobranchiata. *Annals Magazine Natural History*, **18**: 26–42, 83–94.
- King, W. 1850. A Monograph of the Permian Fossils of England. *Palaeontographical Society Monographs*, London. 258 pp.
- Klaamann, E., and Einasto, R. 1982. Coral reefs of the Baltic Silurian (structure, facies relations). p. 35–40. In *Ecostratigraphy of the East Baltic Silurian*. Edited by D. Kaljo and E. Klaamann. Valgus Press, Tallinn. 109 pp.
- Klenina, L.N. 1984. Brachiopody i biostratigrafiya Srednego i Verkhnego Ordovika Chingiz-Tarbagataiskogo megantiklinoriya [Brachiopods and biostratigraphy of the Middle and Upper Ordovician of the Chingiz-Tarbagatai mega-anticline]. p. 6–125. In *Brachiopody i biostratigrafiya Srednego i Verkhnego Ordovika Khrebt Chingiz [Brachiopods and Biostratigraphy of the Middle and Upper Ordovician of the Chingiz Mountain Range]*. Edited by L.N. Klenina, I.F. Nikitin, and L.E. Popov. Akademiya Nauk, Alma Ata. 196 pp.
- Kozłowski, R. 1929. Les brachiopodes gothlandien de la Podolie polonaise. *Palaeontologica Polonica*, **1**: 1–254.
- Krause, A. 1877. Die Fauna der sogen. Beyrichien-oder Chonetenkalkes des norddeutschen Diluviums. *Zeitschrift Deutschen Geologischen Gesellschaft*, **29(1)**: 1–49.
- Kříž, J. 1991. The Silurian of the Prague Basin (Bohemia) — tectonic, eustatic and volcanic controls on facies and faunal development. *Special Papers in Palaeontology*, **44**: 179–203.
- Kříž, J. 1998. Silurian. p. 79–101. In *Palaeozoic of the Barrandian*. Edited by I. Chlupac, V. Havlíček, J. Kříž, Z. Kukal, and P. Štorch. Czech Geological Survey, Prague. 183 pp.
- Kulkov, N.P. 1963. Brachiopody Solovikhinskikh sloev Nizhnego Devona Gornogo Altaya [Brachiopods of the Solovikhin Beds from the Lower Devonian of the Altai Mountains]. *Izdatelstvo Akademiya Nauk SSSR, Moskva*. 131 pp.

- Kulkov, N.P. 1967a. Brachiopody i stratigrafiya Silura Gornogo Altaya [Brachiopods and Stratigraphy of the Silurian of the Altai Mountains]. Akademiya Nauk SSSR, Sibirskoe Otdeleniya Institut Geologii Geofizikii, Nauka, Moskva. 151 pp.
- Kulkov, N.P. 1967b. O rode *Septatrypa* Kozłowski 1929 [On the genus *Septatrypa* Kozłowski 1929]. Doklady Akademii Nauk, **167**: 191–193.
- Kulkov, N.P. 1970. Biostratigraficheskoe sopostavlenie Siluriiskikh otlozhenii Gornogo Altaya i Salaira [Biostratigraphic correlations of Silurian strata of the Altai Mountains and Salair]. Geologiya Geofizika, **6**: 72–79.
- Kulkov, N.P. 1974. Opisanie brachiopod [Brachiopod descriptions]. p. 39–80. In *Rugosy, brachiopody i stratigrafiya Silura Altae-Sayanskoi Gorno Oblasti* [Rugosans, Brachiopods and Silurian Stratigraphy of the Altai-Sayan Mountain Region]. Edited by A.B. Ivanovskii and N.P. Kulkov. Akademiya Nauk, Trudy Institut Geologii Geofizikii, Sibirskoe Otdelenie, **231**: 1–122.
- Kulkov, N.P. 1978. Nekotorye gladkie Spiriferida iz Silura Tuvy [Some Smooth Spiriferids from the Silurian of Tuva]. Fauna i biostratigrafiya verkhnego Ordovika i Silura Altae-Sayanskoe. Nauka, Moskva. pp. 85–94.
- Kulkov, N.P. 1989. Stratigrafiya i brachiopody Ordovika i Nizhnego Silura Gornogo Altaya [Stratigraphy and brachiopods of the Ordovician and Lower Silurian of the Altai Mountains]. Trudy Institut Geologii Geofizikii, Sibirskoe Otdelenie, **717**: 1–224.
- Kulkov, N.P. 1990. Brachiopody i ikh ekologicheskie soobshchestva [Brachiopods and their ecological assemblages]. p. 39–50. In *Silur i Devon yugo-vostoka zapadno-Sibirskoi Plity* [Silurian and Devonian of the Southeastern West Siberian Plate]. Edited by N.P. Kulkov and V.N. Dubatolov. Trudy Institut Geologii Geofizikii, **724**: 1–98.
- Kulkov, N.P., Vladimirovskaya, E.V., and Rybkina, N.L. 1985. Brachiopody i biostratigrafiya verkhnego Ordovika i Silura Tuvy [Brachiopods and biostratigraphy of the Ordovician and Silurian of Tuva]. Trudy Institut Geologii Geofizikii, **635**: 1–208.
- Kunh, A. 1865. Die lösen Versteinerungen im Diluvium vom Tempelhof bei Berlin. Zeitschrift Deutschen Geologischen Gesellschaft, **17**: 311–332.
- Lamont, A. 1978. Pentlandian miscellany: Mollusca, Trilobita, etc. [sic]. Scottish Journal Science, **1**: 245–302.
- Laufeld, S. 1974a. Silurian Chitinozoa from Gotland. Fossils Strata, **5**: 1–130.
- Laufeld, S. 1974b. Reference localities for palaeontology and geology in the Silurian of Gotland. Sveriges Geologiska Undersökning, **C705**: 1–172.
- Laufeld, S., and Bassett, M.G. 1981. The anatomy of a Silurian carbonate platform. Episodes, **1981**: 23–27.
- Laufeld, S., and Jeppsson, L. 1976. Silicification and bentonites in the Silurian of Gotland. Geologiska Föreningens Förhandlingar, **98**: 31–44.
- Laufeld, S., Sundquist, B., and Sjöström, H. 1978. Megapolygonal bedrock structures in the Silurian of Gotland. Sveriges Geologiska Undersökning, **C759**: 5–26.
- Lawson, J.D. 1960. The succession of shelly faunas in the British Ludlovian. Report 21st Session Norden, International Geological Congress, Copenhagen, **7**: 114–125.
- Lawson, J.D. 1975. Ludlow benthonic assemblages. Palaeontology, **18**: 509–525.
- Lenz, A.C. 1968. Two new Lower Devonian atrypid brachiopods from Royal Creek, Yukon Territory, Canada. Journal of Paleontology, **42**(1): 180–185.
- Lenz, A.C. 1978. Upper Silurian and Lower Devonian brachiopods of Royal Creek, Yukon, Canada. Palaeontographica, **A159**: 111–138.
- Lenz, A.C., and Johnson, J.G. 1985. Brachiopods of the Garra Formation (Lower Devonian), Wellington Area, New South Wales, Australia: Rhynchonellida, Spiriferida, Terebratulida. Palaeontographica, **A188**: 71–104.
- Li, W., Rong, J., Dong, D., Yang, D., Su, Y., and Wang, Y. 1985. Silurian and Devonian Rocks of the Bataobao Area in Darhanmumingan Joint Banner, Inner Mongolia. People's Publishing House, Hohhot, Inner Mongolia. 203 pp. [Also cites 1983 and 1984 as publication dates in same volume.]
- Liang, W.P. 1983a. *Eorhynchula* Liang (gen. nov.). p. 284. In *Palaeontological Atlas of East China, Early Paleozoic*. p. 254–286. Edited by D. Liu, H. Xu, and W.P. Liang. Geological Publishing House, Beijing, Vol. 1. 657 pp.
- Liang, W.P. 1983b. *Neorhynchula* Liang (gen. nov.). p. 284–285. In *Palaeontological Atlas of East China, Early Paleozoic*. p. 254–286. Edited by D. Liu, H. Xu, and W. Liang. Geological Publishing House, Beijing, Vol. 1. 657 pp.
- Lin, B. 1984. The Silurian System of China. Stratigraphy of China. Geological Publishing House, Beijing, **6**: 1–245.
- Lindström, G. 1861. Bidrag till kannedomen om Gotlands Brachiopoder. Öfversigt Konglige Vetenskap Akademiens Handlingar, **17**: 337–382.
- Lindström, G. 1880. Brachiopoda. In *Fragmenta silurica e dono Caroli Henrici Wegelin*. Edited by N.P. Angelin and G. Lindström. Samson and Wallin, Holmia. 61 pp.
- Lindström, G. 1882. Anteckningar om Silurlagren på Carlsöarne. Öfversigt Konglige Vetenskaps-Akademiens Förhandlingar, **3**: 15–25.
- Lindström, G. 1885. List of the Fossils of the Upper Silurian Formation of Gotland. Stockholm. 20 pp.
- Lindström, G. 1888. Ueber die Schichtenfolge des Silur auf der Insel Gotland. Neues Jahrbuch Mineralogie Geologie Petrefaktkunde, **1**: 147–165.
- Linnaeus, C.F. 1753. Museum Tessenianum, Stockholm. 13 pp.
- Linnaeus, C.F. 1758. Systema naturae, sive regna tria naturae systematice proposita classes, ordines, genera et species. Edition 10, Tome 1, Regnum animale, reformata, Stockholm. 824 pp.
- Lopushinskaya, T.V. 1965. O novykh brachiopodakh iz Siluriiskikh otlozhenii Sibirskoi Platformy [On new brachiopods from the Silurian deposits of the Siberian Platform]. Trudy Sibirskogo Nauchno-issledovatel'skogo Institut Geologii, Geofizikii i Mineral'nogo Sibiry [SNIIGGIMS], **34**: 23–34.
- Lopushinskaya, T.V. 1976. Brachiopody i stratigrafiya Siluriiskikh otlozhenii severa Sibirskoi Platformy [Brachiopods and stratigraphy of Silurian strata from the northern Siberian Platform]. Trudy Sibirskogo Nauchno-issledovatel'skogo Institut Geologii, Geofizikii Mineral'nogo Sibiry [SNIIGGIMS], **199**: 1–95.
- Lundqvist, G., Hede, J.E., and Sundius, N. 1940. Beskrivning till Kartbladet Visby och Lummelunda. Sveriges Geologiska Undersökning, **Aa183**: 1–167.
- MacKinnon, D.I. 1991. A fresh look at growth of spiral brachidia. p. 147–153. In *Brachiopods Through Time*. Edited by D.I. MacKinnon, D.E. Lee, and J.D. Campbell. Balkema Press, Rotterdam. 447 pp.
- Manten, A.A. 1971. Silurian reefs of Gotland. Developments in Sedimentology, **13**: 1–539.
- Marr, J.E., and Nicholson, H.A. 1888. The Stockdale Shales. Quarterly Journal of the Geological Society, London, **44**: 654–726.
- Martinsson, A. 1962. Ostracodes of the Family Beyrichiidae from the Silurian of Gotland. Bulletin Geological Institution University Uppsala, **46**: 1–369.
- Martinsson, A. 1967. The succession and correlation of ostracod faunas in the Silurian of Gotland. Geologiska Föreningens Förhandlingar, **89**: 150–386.
- McChesney, J.H. 1868. Descriptions of fossils from the Palaeozoic rocks of the western states, with illustrations. Transactions of the Chicago Academy Sciences, **1**: 1–57.
- McEwan, E.D. 1939. Convexity of articulate brachiopods as an aid in identification. Journal of Paleontology, **13**: 617–620.

- McKerrow, W.S. 1979. Ordovician and Silurian changes in sea level. *Journal of the Geological Society (London)*, **136**: 137-145.
- M'Coy, F. 1851. On some new Cambro-Silurian fossils. *Annals of the Magazine of Natural History*, **8**: 387-409.
- M'Coy, F. 1855. A Synopsis of the Classification of the British Palaeozoic Rocks, with a Systematic Description of the British Palaeozoic Fossils in the Geological Museum of the University of Cambridge [in part with A. Sedgwick]. Parker and Son, London. 661 pp.
- Menakova, G.N. 1964. Brakhiopody iz nizhnasiluriiskikh otlozhenii Zeravshano-Gissarskoi Gornoi Oblasti [Brachiopods from the Lower Silurian of the Zeravshan-Gissar Mountain region]. *Trudy Upravleniya Geologii Okhrany Nedr, Sovete Ministrovo Tadzhikskoi SSR, Paleontologiya Stratigrafiya*, **1**: 3-51.
- Menakova, G.N., and Nikiforova, O.I. 1986. Novye verkhnie Siluriiskie brakhiopody khrebtta Zeravshan-Gissar [New Upper Silurian brachiopods from the Zeravshan-Gissar Mountain Range]. *Paleontologicheskii Zhurnal*, **1986(4)**: 65-76.
- Misius, P.P. 1984. *Kuzgunia* Misius 1969. p. 113. [From unpublished author's preprint dated 1969.] In Brakhiopody i biostratigrafiya Srednego i Verkhnego Ordovika Chingiz-Tarbagataiskogo megantiklinoriya [Brachiopods and Biostratigraphy of the Middle and Upper Ordovician of the Chingiz-Tarbagatai Mega-anticline]. Edited by L.N. Klenina. p. 6-125. In Brakhiopody i biostratigrafiya Srednego i Verkhnego Ordovika Khrebtta Chingiz [Brachiopods and Biostratigraphy of the Middle and Upper Ordovician of the Chingiz Mountain Range]. Edited by L.N. Klenina, I.F. Nikitin, and L.E. Popov. Akademiya Nauk, Alma Ata. 196 pp.
- Misius, P.P. 1986. Brakhiopody Ordovika severnoi Kirgizii [Ordovician Brachiopods from Northern Kirgizia]. Akademiya Nauk Kirgizskoi SSR, Institut Geologii, Frunze. 253 pp. [Author's preprint dated 1969.]
- Mitchell, J., and Dun, W.S. 1920. The Atrypidae of New South Wales, with references to those recorded from other states of Australia. *Proceedings Linnaean Society New South Wales*, **1920(2)**: 266-276.
- Mizens, L.I. 1977. Novye Siluriiskie atripidy vostochnogo sklona severnogo i srednego Urala [New Silurian atrypids from the eastern slopes of the northern and central Urals]. *Trudy Institut Geologii Geokhimii*, **129**: 39-55.
- Mizens, L.I. 1981. Nekotorye nizhnasiluriiskie i ludlovskie atripidy zapadnogo sklona srednego Urala [Some Lower Silurian and Ludlovian Atrypids of the Western Slopes of the Central Urals]. p. 41-51. In Biostratigrafiya i fauna srednego Paleozoya Urala [Biostratigraphy and Fauna of the Middle Paleozoic of the Urals]. Edited by V.P. Sapelnikov and B.I. Chuvashov. Akademiya Nauk, Uralskii Nauchnyi Tsentr, Sverdlovsk. 128 pp.
- Mizens, L.I. 1985. Novye podrody roda *Atrypodea* (Brachiopoda) [New subgenera of the genus *Atrypodea* (Brachiopoda)]. *Ezhegodnik Institut Geologii i Geokhimii, Sverdlovsk*, **1984**: 10.
- Mizens, L.I., and Sapelnikov, V.P. 1982. Rebristye siluriiskie i lochkovskie atripidy vostochnogo sklona Urala [Ribbed Silurian and Lochkovian Atrypids from the Eastern Slopes of the Urals]. Akademiya Nauk SSSR, Uralskii Nauchnyi Tsentr, Sverdlovsk. 43 pp. [Labeled preprint.]
- Mizens, L.I., and Sapelnikov, V.P. 1985. Podrod *Globatrypa* Mizens et Sapelnikov, subgen. nov. [Subgenus *Globatrypa* Mizens et Sapelnikov, subgen. nov.]. p. 10. In Novye podrody roda *Atrypodea* (Brachiopoda) [New Subgenera of the Genus *Atrypodea* (Brachiopoda)]. Edited by L.I. Mizens. *Ezhegodnik Institut Geologii i Geokhimii, Sverdlovsk*, **1984**: 10.
- Modzalevskaya, T.L. 1968. Atlas Siluriiskoi i Rannedevonskoi fauny Podolii [Atlas of Silurian and Early Devonian Fauna of Podolia]. Vsesoyuznyi Nauchno-issledovatel'skogo Geologicheskii Institut, Ministerstvo Geologii SSSR, VSEGEI, Leningrad. 37 pl.
- Modzalevskaya, T.L. 1980. Brakhiopody Silura i Nizhnego Devona i ikh stratigraficheskoe znachenie [Silurian and Lower Devonian brachiopods and their stratigraphic distribution]. p. 82-104. In Siluriiskie i Nizhnedevonskie otlozheniya ostrova Dolgogo [Silurian and Lower Devonian Strata of Dolgo Island]. Edited by V.P. Sapelnikov. Akademiya Nauk, Uralskii Nauchnyi Tsentr, Sverdlovsk. 143 pp.
- Modzalevskaya, T.L. 1981. Brakhiopody Pozdnego Silura i Rannego Devona Pripolyarnogo Urala i Gryady Chernysheva [Late Silurian and Early Devonian brachiopods of the Prepolars Urals and the Chernyshev Range]. *Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshestva*, **24**: 173-204.
- Modzalevskaya, T.L., and Nikiforova, O.I. 1982. Brakhiopody Skalskogo gorizonta Podolii [Brachiopods of the Skala Horizon in Podolia]. *Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshestva*, **25**: 98-121.
- Moore, R.C. 1952. Brachiopods. p. 197-267. In *Invertebrate Fossils*. Edited by R.C. Moore, C.G. Lalicker, and A.G. Fischer. McGraw-Hill, New York. 766 pp.
- Munnecke, A., and Samtleben, C. 1996. The formation of micritic limestones and the development of limestone-marl alterations in the Silurian of Gotland, Sweden. *Facies*, **34**: 159-176.
- Munnecke, A., Westphal, H., Reijmer, J.J.G., and Samtleben, C. 1997. Microspar development during early marine burial diagenesis: a comparison of Pliocene carbonates from the Bahamas with Silurian limestones from Gotland (Sweden). *Sedimentology*, **44**: 997-990.
- Münster, G. 1840. Die Versteinerungen des Uebergangskalkes mit Clymenien und Orthoceratiten von Oberfranken. Beiträge zu Petrefaktenkunde von Herrn V. Meyer und Georg Graf zu Münster. Buchner Buchhandlung, Bayreuth. pp. 33-121.
- Munthe, H. 1911. On the sequence of strata within southern Gotland. *Geologiska Föreningens Förhandlingar*, **32**: 1397-1453. [On the front leaf, publication dated May, 1910.]
- Munthe, H. 1921. Beskrivning till Kartbladet Burgsvik, Jämt, Höbörge och Ytterholmen. Sveriges Geologiska Undersökning, **Aa152**: 1-172.
- Munthe, H., Hede, J.E., and Post, L. von. 1925a. Beskrivning till Kartbladet Ronhamn. Sveriges Geologiska Undersökning, **Aa156**: 1-96.
- Munthe, H., Hede, J.E., and Post, L. von. 1925b. Gotlands geologi en översikt. Sveriges Geologiska Undersökning, **C331**: 1-30.
- Munthe, H., Hede, J.E., and Lundqvist, P. 1927a. Beskrivning till Kartbladet Klintehamn. Sveriges Geologiska Undersökning, **Aa169**: 1-65.
- Munthe, H., Hede, J.E., and Post, L. von. 1927b. Beskrivning till Kartbladet Hemse. Sveriges Geologiska Undersökning, **Aa164**: 1-155.
- Munthe, H., Hede, J.E., and Lundqvist, P. 1928. Beskrivning till Kartbladet Slite. Sveriges Geologiska Undersökning, **Aa169**: 1-130.
- Munthe, H., Hede, J.E., and Lundqvist, P. 1929. Beskrivning till Kartbladet Katthammarvik. Sveriges Geologiska Undersökning, **Aa170**: 1-120.
- Munthe, H., Hede, J.E., and Lundqvist, P. 1933. Beskrivning till Kartbladet Kappelshamn. Sveriges Geologiska Undersökning, **Aa171**: 1-82.
- Munthe, H., Hede, J.E., and Lundqvist, P. 1936. Beskrivning till Kartbladet Färö. Sveriges Geologiska Undersökning, **Aa180**: 1-82.
- Murchison, R.I. 1833. On the sedimentary deposits which occupy the western parts of Shropshire and Herefordshire, and are prolonged from NE to SW, through Radnor, Montgomery, Caermarthen, Brecon, Pembroke, Monmouth, Gloucester and Stafford; with descriptions of the coalfields and overlying formations. *London Edinburgh Philosophical Magazine*, **3**: 224-231.
- Murchison, R.I. 1839. The Silurian System. John Murray, London. 768 pp., 37 pl. [Plates to Sowerby 1839.]

- Murchison, R.I. 1847. On the Silurian and associated rocks in Dalecarlia, and on the succession from Lower to Upper Silurian in Smoland, Öland and Gothland, and in Scania. Quarterly Journal of the Geological Society, London, **3**: 1–48.
- Musteikis, P. 1991. Siluriiskie soobshestva brachiopod v razreze skv. Vilkavishkis-129 [Silurian brachiopod associations from beds of the Vilkavishkis-129 borehole]. Nauchnye Trudy Uchenykh Zavedenii Litvy Geologija, **12**: 47–66.
- Musteikis, P. 1993. Silurian brachiopod communities in the section of the Pilviskiai-141 borehole. Geologija, **14**: 118–129.
- Musteikis, P., and Juskute, V. 1999. Late Silurian brachiopod communities from western Lithuania. Geologija, **27**: 10–25.
- Musteikis, P., and Modzalevskaya, T.L. 2002. Some Silurian brachiopods from Lithuania and their palaeobiogeographical significance. Palaeontology, **45**: 595–626.
- Musteikis, P., and Paskevicius, J.J. 1999. Brachiopod communities of the Lithuanian Silurian. p. 305–326. In *Paleocommunities: A Case Study from the Silurian and Lower Devonian*. Edited by A.J. Boucot and J.D. Lawson. Cambridge University Press, Cambridge. 895 pp.
- Nalivkin, D.V. 1926. Oчерк геологии Туркестана [Outline of the geology of Turkestan]. Akademiya Nauk, Tashkent and Moskva. 184 pp.
- Nalivkin, D.V. 1960. Novye vidye Devonskikh atripid i spiriferid Arktiki [New species of Devonian atrypids and spiriferids of the Arctic]. In *Novye vidye drevnikh rastenyi i bespozvonochnykh SSSR* [New Species of Ancient Plants and Invertebrates of the USSR]. Edited by B.P. Markovskii. Trudy VSEGEI, **1960**: 380–382.
- Nestor, H. 1995. Ordovician and Silurian reefs in the Baltic area. Publications Service Géologique Luxembourg, **29**: 39–47.
- Nestor, H. 1997. Silurian. p. 89–106. In *Geology and Mineral Resources of Estonia*. Edited by A. Raukas and A. Teedumäe. Estonian Academy Publishers, Tallinn. 436 pp.
- Nestor, H., and Einasto, R.E. 1977. Facies-sedimentary model of the Silurian Paleobaltic pericontinental basin. p. 89–121. In *Facies and Fauna of the Baltic Silurian*. Edited by D. Kaljo. Akademiya Nauk, Tallinn. 286 pp.
- Nettelroth, H. 1889. Kentucky Fossil Shells. A Monograph of the Fossil Shells of the Silurian and Devonian Rocks of Kentucky. Kentucky Geological Survey, Frankfort, Kentucky. 245 pp.
- Neumann, B.E.E., and Kershaw, S. 1991. Gotland/Sweden, Silurian Reefs and Coral Bearing Strata. Guidebook VI International Symposium on Fossil Cnidaria, Including Archeocyatha and Porifera, Excursion A1. University Bergen, Bergen. 111 pp.
- Nikiforova, O.I. 1949. Polevoi atlas rukovodyashchikh brachiopod Verkhnego Silura Kirgizskoi SSR [Field Atlas of Index Brachiopods for the Upper Silurian of Kirgiz SSR]. Kirgizskii Filial Akademii Nauk SSSR, Geologicheskii Institut, Frunze. 51 pp.
- Nikiforova, O.I. 1954. Stratigrafiya Ordovika i Silura Sibirskoi Platformy i ee paleontologicheskoe obosnovanie (Brachiopody) [Ordovician and Silurian stratigraphy of the Siberian Platform and its paleontological basis (Brachiopods)]. Trudy VSEGEI, **56**: 1–412.
- Nikiforova, O.I. 1961. Paleontological part. p. 67–284. In *Stratigrafiya i brachiopody siluriiskikh otlozhenii Podolii* [Stratigraphy and Brachiopods of the Silurian Strata of Podolia]. Edited by O.I. Nikiforova and O.N. Andreeva. Trudy VSEGEI, Leningrad. 218 pp.
- Nikiforova, O.I. 1970. Brachiopody Grebenskogo Gorizonta Vaigacha (Pozdniy Silur) [Brachiopods of the Greben Horizon of Vaigach (Late Silurian)]. p. 97–149. In *Stratigrafiya i fauna Siluriiskikh otlozhenii Vaigach* [Stratigraphy and Fauna of Silurian Strata of Vaigach]. Edited by S.V. Cherkasova. Nauchno-issledovatel'skii Institut Geologii Arktiki, Leningrad. 237 pp.
- Nikiforova, O.I. 1978. Brachiopody Chasmankalonskikh, Archalykskikh i Minkucharskikh sloev [Brachiopods of the Chasmankalon, Archalyk and Minkuchar Beds]. p. 102–125. Edited by B.S. Sokolov and E.A. Elkin. Trudy Sibirskoe Otdelenie, Institut Geologii Geofizikii, **397**: 1–224.
- Nikiforova, O.I., and Modzalevskaya, T.L. 1968. Nekotorye Llandoveryiskie i Venlovskie brachiopody severo-zapadnoi chasti Sibirskoi Platformy [Some Llandovery and Wenlock brachiopods from the northwestern part of the Siberian Platform]. NIIGA Uchenye Zapiski, **21**: 50–81.
- Nikiforova, O.I., Modzalevskaya, T.L., and Bassett, M.G. 1985. Review of the Upper Silurian and Lower Devonian articulate brachiopods of Podolia. Special Papers in Palaeontology, **34**: 1–66.
- Norford, B.S. 1962a. Illustrations of Canadian fossils, Cambrian, Ordovician and Silurian of the western Cordillera. Geological of Survey Canada Paper, **62-14**: 1–25.
- Norford, B.S. 1962b. The Silurian fauna of the Sandpile Group of northern British Columbia. Geological Survey of Canada Bulletin, **78**: 1–51.
- Olenicheva, M.A. 1983. Verkhnesiluriiskie brachiopody Pribalkhash [Upper Silurian brachiopods of Balkhash]. p. 135–153. In *Stratigrafiya i paleontologiya Nizhnego Paleozoya Kazakhstana* [Lower Paleozoic Stratigraphy and Paleontology of Kazakhstan]. Edited by R.K. Danilenko. Nauka, Alma Ata. 176 pp.
- Olenicheva, M.A. 1986. Brachiopody [Brachiopods]. p. 61–74. In *Balkhashskii Segment, Tokrauskii Gorizont verkhnego Silura* [Balkhash Segment, Tokrau Horizon Upper Silurian]. Edited by S.M. Bandaletov, T.N. Koren, and L.M. Paletz. Ministerstvo Geologii Kazakhskoi SSR, Alma Ata. 236 pp.
- Opik, A.A. 1953. Lower Silurian fossils from the Iläenus Band, Heathcote, Victoria. Memoirs Victoria Geological Survey, **19**: 1–42.
- Oradovskaya, M.M. 1975. Superfamily Atrypacea. p. 102–118. In *Polevoi atlas Siluriiskoi fauny Severo-vostoka SSSR* [Field Atlas of Silurian Fauna of Northeastern USSR]. Edited by A.A. Nikolaev, M.M. Oradovskaya, B.V. Preobrazhenskii, A.F. Abushik, E.I. Myagkova, A.M. Obut, R.F. Sobolevskaya, and V.V. Kovekhor. Magadanskoe Knizhnoe Izdatel'stvo, Magadan. 192 pp.
- Oradovskaya, M.M. 1982. Rod *Euroatrypa* Oradovskaya gen. nov. p. 63–64. In *Novye Ordovikskie Atrypid (Brachiopoda) severo-vostoka SSSR, Taimyra i Kazakhstana* [A New Ordovician Atrypid (Brachiopoda) from Northeastern USSR, Taimyr and Kazakhstan]. Edited by O.I. Nikiforova, M.M. Oradovskaya, and L.E. Popov. Paleontologicheskii Zhurnal, **1982(3)**: 62–69.
- Oradovskaya, M.M. 1983. Brachiopoda. p. 35–73. In *Granitsa Ordovika i Silura na severo-vostoke SSSR* [Ordovician and Silurian Boundary in the Northeastern USSR]. Edited by T.N. Koren, M.M. Oradovskaya, and R.F. Sobolevskaya. Trudy Ministerstva Geologii, Mezhdromstvennyi Stratigraficheskii Komitet, **11**: 1–208.
- Orbigny, A. d'. 1847. Considérations zoologiques et géologiques sur les brachiopodes ou palliobranches. Comptes Rendus Hebdomaire Séances, Académie Sciences, Paris. Série **2(25)**: 193–195.
- Orbigny, A. d'. 1850. Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnés faisant suite au cours élémentaire de paléontologie et de géologie stratigraphique, **1(1849)**: 1–394.
- Parkinson, J. 1833. Organic Remains of a Former World. An examination of the mineralized remains of the vegetables and animals of the Antediluvian world, generally termed extraneous fossils. Nattali, London, Vol. 3. 467 pp.
- Penn, I.E. 1970. The Brachiopod Chronospecies *Atrypa reticularis* (Linnaeus). Unpublished Ph.D. thesis. University of Glasgow, Glasgow. 163 pp.
- Penn, J.S.W. 1971. Bioherms in the Wenlock Limestone of the Malvern area (Herefordshire, England). Mémoires Bureau Recherches Géologiques Minéralogiques, **73**: 129–137.
- Penn, J.S.W., and French, J. 1971. The Malvern Hills. Geologists' Association Guides, **4**: 1–36.

- Percival, I.G. 1991. Late Ordovician brachiopods from central New South Wales. *Memoirs Association Australasian Palaeontologists*, **11**: 107–177.
- Perry, D.G. 1984. Brachiopoda and biostratigraphy of the Silurian-Devonian Delorme Formation in the District of Mackenzie, the Yukon. *Royal Ontario Museum Life Sciences Contributions*, **138**: 1–243.
- Philip, G.M. 1962. The paleontology and stratigraphy of the Siluro-Devonian sediments of the Tyers area, Gippsland, Victoria. *Proceedings Royal Society Victoria*, **75**: 123–246.
- Plodowski, G. 1971. Glattschalige Atrypacea aus den Zentral-karnischen Alpen und aus Böhmen. *Senckenbergiana Lethaea*, **52**: 285–313.
- Plodowski, G. 1976. Die Brachiopoden des Silur/Devon-Grenz-profils von Eggenfeld (Grazer Paläozoikum). *Mitteilungen Abteilung Geologie Paläontologie Bergbau Landesmuseum Joanneum*, **37**: 36–51.
- Popov, L.E., Nikitin, I.F., and Sokiran, E.V. 1999. The earliest smooth atrypids and athyrids (Brachiopoda) from the Ordovician of Kazakhstan. *Palaeontology*, **42**: 625–661.
- Poulsen, C. 1943. The fauna of the Ofley Island Formation, Part II. Brachiopoda. *Meddelelser om Grønland*, **72**: 1–60.
- Quenstedt, F.A. 1852. *Handbuch der Petrefactenkunde*. Laup-p'schen Buchhandlung, Tübingen. 982 pp.
- Quenstedt, F.A. 1867. *Handbuch der Petrefactenkunde*. Laup-p'schen Buchhandlung, Tübingen. 982 pp., atlas 86 pl. [2nd ed.]
- Quenstedt, F.A. 1882. *Handbuch der Petrefactenkunde*. Laup-p'schen Buchhandlung, Tübingen. 1238 pp., 443 figs. [3rd ed.]
- Ramsköld, L. 1984. Silurian odontopleurid trilobites from Gotland. *Palaeontology*, **27**: 239–264.
- Ramsköld, L. 1986. Silurian encrinurid trilobites from Gotland and Dalarna, Sweden. *Palaeontology*, **29**: 527–575.
- Ratcliffe, K.T. 1988. Oncoids as environmental indicators in the Much Wenlock Limestone Formation of the English Midlands. *Journal of the Geological Society (London)*, **145**: 117–124.
- Ratcliffe, K.T., and Thomas, A.J. 1999. Carbonate depositional environments in the late Wenlock of England and Wales. *Geological Magazine*, **136**: 189–204.
- Reed, F.R.C. 1895. Brachiopods (Fossil). *Cambridge Natural History*, **3**: 491–512.
- Reed, F.R.C. 1897. The fauna of the Keisley Limestone, Part II. Conclusion. *Quarterly Journal of the Geological Society, London*, **53**: 67–106.
- Reed, F.R.C. 1908. Sedgwick Museum notes: new fossils from the Haverford-west District. *Geological Magazine*, **5**: 433–437.
- Reed, F.R.C. 1936. The Lower Palaeozoic faunas of the southern Shan States. *Memoirs Geological Survey India*, **21**: 1–183.
- Reed, F.R.C. 1944. Notes on some new Ordovician brachiopods from Girvan. *Annals Magazine Natural History*, **11**: 215–222.
- Richter, R. 1866. Aus dem thüringischen Schiefergebirge. *Zeitschrift Deutschen Geologischen Gesellschaft*, **18**: 409–425, pl. 5–6.
- Riding, R. 1981. Composition, structure and environmental setting of Silurian bioherms and biostromes in northern Europe. *Special Publications Society Economic Paleontologists Mineralogists*, **30**: 41–83.
- Riding, R., and Watts, N.R. 1991. The lower Wenlock reef sequence of Gotland: facies and lithostratigraphy. *Geologiska Föreningens Förhandlingar*, **113**: 343–372.
- Roemer, F. 1861. Die fossile Fauna der silurischen Diluvial-Geschiebe von Sadewitz bei Oels in Nieder-Schlesien. Fünfzig-jährigen Jubiläums Königlich Universität Breslau, R. Nischkowsky, Breslau. 81 pp.
- Roemer, F. 1862. Ueber die Diluvial-Geschiebe von nordischen Sedimentär-Gesteine in der norddeutschen Ebene und im besonderen über die verschiedenen durch dieselben vertretenen Stockwerke oder geognostischen Niveaus der Paläozoischen Formation. *Zeitschrift Deutschen Geologischen Gesellschaft*, **14**(3): 575–637.
- Roemer, F. 1866. Beiträge zur geologischen Kenntniss des nord-deutschen Harzgebirges. *Palaeontographica*, **13**(5): 201–235. [No plates.]
- Roemer, F. 1876. *Lethaea Geognostica*, Theil 1, Lethaea Palaeozoica. Henzler, Stuttgart. 323 pp., atlas 62 pl.
- Roemer, F. 1885. Lethaea erratica oder Aufzählung und Beschreibung der in der norddeutschen Ebene vorkommenden Diluvial-Geschiebe nordischer Sedimentär-Gesteine. *Paläontologische Abhandlungen*, **2**(5): 1–173, Leipzig.
- Rong, J., and Yang, X. 1980. Brachiopods from the Miaokao Formation (Upper Silurian) of Qujing, eastern Yunnan. *Acta Palaeontologica Sinica*, **19**: 263–288.
- Rong, J., and Yang, X. 1981. Middle and late Early Silurian brachiopod faunas in southwest China. *Memoirs Nanjing Institute Geology Palaeontology*, **13**: 163–220.
- Rong, J., and Zhang, Z. 2001. Brachiopoda. p. 88–102. *In* Silurian and Early Devonian Stratigraphy and Faunas in Southern Tian Shan, Xinjiang, China University Science Technology, Hefei. 130 pp.
- Rong, J., Xu, H., and Yang, X. 1974. Brachiopods. p. 195–208. *In* Handbook of Stratigraphy and Paleontology of China. Scientific Publishing House, Beijing. 454 pp.
- Rong, J., Su, Y., and Li, W. 1983. Brachiopods of the Xibiehe Formation (Upper Silurian) in Darhanmumingan Joint Banner, Inner Mongolia. p. 27–55. *In* Silurian and Devonian Rocks of the Bataobao Area in Darhanmumingan Joint Banner, Inner Mongolia. Edited by W. Li, J. Rong, and D. Dong. People's Publishing House, Hohhot, Inner Mongolia. 184 pp. [Also cites dates 1984 and 1985 for same volume.]
- Rong, J., Zhang, Y., and Chen, X. 1987. Pridolian and Lochkovian brachiopods from the Luqu-Tewo area of the western Qinling Mountains, China. *In* Late Silurian-Devonian Strata and Fossils from the Luqu-Tewo Area of the Western Qinling Mountains, China. Nanjing Institute Geology Paleontology, Nanjing, Vol. 2. 94 pp.
- Rothpletz, A. 1913. Über die Kalkalgen, Spongiostromen und einige andere Fossilien aus dem Obersilur Gotlands [sic]. *Sveriges Geologiska Undersökning*, **Ca10**: 1–57.
- Rozman, Kh. S. 1986. Osnovnye cherty zoogeografii Ordovika i Silura Mongolii po brachiopodam [Main zoogeographic characters of the Ordovician and Silurian of Mongolia based on brachiopods]. *Joint Soviet-Mongolian Expeditions*, **29**: 55–70.
- Rozman, Kh. S. 1988. Nove silurijskie brachiopody [New Silurian brachiopods]. *Joint Soviet-Mongolian Expeditions*, **33**: 23–51.
- Rubel, M. 1970. Pentamerid and Spiriferid Brachiopods from the Silurian of Estonia. *Eesti Teaduste Akadeemia Toimetised, Valgus*, Tallinn. 75 pp.
- Rubel, M. 1977. Reviziya brachiopod Dayiacea iz Silur Pribaltiki [Revision of Dayiacea brachiopods from the Silurian of the Pribaltic]. *Eesti Teaduste Akadeemia Toimetised*, **26**: 211–220.
- Rubel, M., and Roomusoks, A. 1970. Brachiopody [Brachiopods]. p. 139–150. *In* Silur Estonii [Silurian of Estonia]. Edited by D. Kaljo. Valgus, Tallinn. 343 pp.
- Rubel, M., Brazauskas, A., Musteikis, P., and Puura, I. 1991. Distribution of Wenlock brachiopods in the Suuriku section, Estonia. *Eesti Teaduste Akadeemia, Toimetised Keemia Geoloogia*, **40**: 69–73.
- Rukavishnikova, T.B. 1982. Drevnie atripidy Kazakhstana [Ancient atrypids of Kazakhstan]. p. 45–46. *In* Nove Danyie po Sistematike i Morfogenezu Rannepaleozoiskikh Brachiopod [New Data on the Systematics and Morphogenesis of Early Paleozoic Brachiopods]. Edited by A.N. Khodalevich. Akademiya Nauk SSSR, Uralskii Nauchnyi Tsentr, Sverdlovsk.
- Rybikina, N.L. 1985. Brachiopods (partim). p. 42–48, 162–166. *In* Brachiopody i biostratigrafiya verkhnego Ordovika i Silura

- Tuvy [Brachiopods and Stratigraphy of the Ordovician and Silurian of Tuva]. Edited by N.P. Kulkov, E.V. Vladimirovskaya, and N.L. Rybkina. Trudy Institut Geologii Geofizikii, **635**: 1-208.
- Rybnikova, M.V. 1967. Opisanie brachiopod [Brachiopod descriptions]. p. 169-122. In Stratigrafiya, fauna i usloviya obrazovaniya siluriiskikh porod srednei Pribaltiki [Stratigraphy, Fauna and Conditions of Deposition of the Silurian Rocks of the Central Prebaltic]. Edited by L.K. Gailite, M.V. Rybnikova, and R.Z. Ulst. Akademiya Nauk, Vilnius. 554 pp.
- Rzhonsnitskaya, M.A. 1960. Order Atrypida, p. 257-264, pl. 53-56. In Osnovy paleontologii, Mshanki, Brachiopody [Treatise of Paleontology, Bryozoans, Brachiopods]. Edited by T.G. Sarycheva. Izdatelstvo Akademiya Nauk SSSR, Moskva. 343 pp.
- Rzhonsnitskaya, M.A. 1964. O Devonskikh atripidakh Kuznetskogo basseina [On Devonian atrypids from the Kuznetsk Basin]. Trudy Vsesoyuznyi Nauchno-issledovatel'skii Geologicheskii Institut [VSEGEI], **93**: 91-112.
- Rzhonsnitskaya, M.A. 1968. Novye vidy Devonskikh atripid okhrani Kuznetskogo basseina [New Devonian atrypid species from the outskirts of the Kuznetsk Basin]. In Novye vidy drevnykh Rastenii i Bespozvonochnykh SSSR. Edited by B.S. Sokolov. Akademiya Nauk, Moskva, **2**: 130-149.
- Rzhonsnitskaya, M.A. 1974. Subfamily Spirigerininae, p. 57. In Materialy po faune i flore Dzhidalskoi Svity (Srednii Paleozoi Alaiskii Khrebet) [Materials on the Fauna and Flora of the Dzhidalin Suite (Middle Paleozoic of the Alai Mountains)]. Edited by Yu. Biske, Yu., B.V. Goryanov, N.M. Petrosyan, and M.A. Rzhonsnitskaya. Voprosii Stratigrafii, **1974**: 44-71.
- Rzhonsnitskaya, M.A. 1975. Biostratigrafiya devona okranii Kuznetskogo Basseina [Biostratigraphy of the Devonian outskirts of the Kuznetsk Basin]. Trudy Vsesoyuznyi Nauchno-issledovatel'skii Geologicheskii Institut (VSEGEI), Novaya Seriya, **244**: 1-232.
- Salter, J.W. 1873. A Catalogue of the Collection of Cambrian and Silurian Fossils Contained in the Geological Museum of the University of Cambridge. University Press, Cambridge. 204 pp.
- Saltzman, M.R. 2001. Silurian $\delta^{13}C$ stratigraphy: a view from North America. Geology, **29**: 671-674.
- Samtleben, C. 1972. Feinbau und Wachstum von Spiriferiden-Armgerüsten. Paläontologische Zeitschrift, **46**: 20-33.
- Samtleben, C. 1975. Zum Schalenbau von Spiriferen-Armgerüsten. Mitteilungen Geologisches-Paläontologisches Institut Universität Hamburg, **44**: 217-244.
- Samtleben, C., and Munnecke, A. 1999. Reefmounds im unteren Wenlock auf Gotland: Beispiele früher Korallenriffe. Meyeniana, **51**: 77-94.
- Samtleben, C., Munnecke, A., Bickert, T., and Pätzold, J. 1996. The Silurian of Gotland (Sweden): facies interpretation based on stable isotopes in brachiopod shells. Geologische Rundschau, **85**: 278-292.
- Samtleben, C., Munnecke, A., and Bickert, T. 2000. Development of facies and C/O-isotopes in transects through the Ludlow of Gotland: evidence for global and local influences on a shallow-marine environment. Facies, **43**: 1-38.
- Sapelnikov, V.P. 1956. Nekotorye novye brachiopody iz siluriiskikh otlozhenii Nizhne Serginskogo raiona zapadnogo sklona Urala [Some new brachiopods from Silurian strata of the Lower Sergin region on the western slopes of the Urals]. Nauchnye Raboty Studentov Sverdlovskogo Gornogo Instituta, **2**: 5-13.
- Sapelnikov, V.P. 1960. Otryad Atrypida, p. 376-379. In Novye vidy drevnykh rastenii i bespozvonochnykh SSSR. Edited by B.P. Markovskii, Vsegei, Leningrad, **1960**: 1-632.
- Sapelnikov, V.P. 1964. Siluriiskie karinatiniiny vostochnogo sklona Urala [Silurian carinatiniids from the eastern slopes of the Urals]. Trudy Sverdlovskogo Gornogo Instituta Imeni V.V. Bakhrusheva, **45**: 5-13.
- Sapelnikov, V.P., and Mizens, L.I. 1982. Gladkie siluriiskie atripidy vostochnogo sklona srednego i severnogo Urala [Smooth Silurian Atrypids from the Eastern Slopes of the Central and Northern Urals]. Akademiya Nauk SSSR, Uralskii Nauchnyi Tsentr, Sverdlovsk. 52 pp.
- Sapelnikov, V.P., and Mizens, L.I. 1991. Atlas rukovodyashchikh vidov Siluriiskikh brachiopod Urala [Atlas of Guide Species of Silurian Brachiopods of the Urals]. Akademiya Nauk, Uralskoe Otdelenie, Sverdlovsk. 272 pp.
- Sapelnikov, V.P., Mizens, L.I., and Shatrov, V.P. 1987. Stratigrafiya i brachiopody verkhnesiluriiskikh-srednedevonskikh otlozhenii severa vostochnogo sklona Urala [Stratigraphy and Brachiopods of the Upper Silurian-Middle Devonian Strata of the Northeastern Slopes of the Urals]. Akademiya Nauk, Moskva. 223 pp.
- Savage, N.M. 1970. New atrypid brachiopods from the Lower Devonian of New South Wales. Journal of Paleontology **44**(4): 665-668.
- Schlottheim [sic, corrected = Schlothheim], E.F. von. 1813. Beiträge zur Naturgeschichte der Versteinerungen in geognostischer Hinsicht. Taschenbuch für die gesammte Mineralogie mit Hinsicht auf die neuesten Entdeckungen. Hermann, Frankfurt am Main, **7**(1): 3-134.
- Schmidt, F. 1858. Beitrag zur Geologie der Insel Gotland. Archiv Naturkunde Livland, Esthland, Kurland, **2**: 1-64.
- Schmidt, F. 1859. Untersuchungen über die Silurische Formation von Esthland, Nord-Livland und Oesel. Archiv Naturkunde Livland, Esthland, Kurland, **2**: 65-247.
- Schmidt, F. 1875. Einige Bemerkungen über die Podolisch-Galizische Formation und deren Petrefakten. Zapiskie Imperatorskago Mineralogicheskago Obshestva, St. Petersburg. 21 pp.
- Schuchert, C., and Cooper, G.A. 1930. Upper Ordovician and Lower Devonian stratigraphy and paleontology from the Percé region of Québec. American Journal Science, **20**: 265-288.
- Schuchert, C., and Levene, C.M. 1929. Brachiopoda. Fossilium Catalogus, 1, Animalia, Pars 42. Junk, Berlin. 140 pp.
- Scoffin, T.P. 1971. The conditions of growth of the Wenlock reefs of Shropshire (England). Sedimentology, **17**: 173-219.
- Scoffin, T.P. 1972. Cavities in the reefs of the Wenlock Limestone (Mid-Silurian) of Shropshire, England. Geologische Rundschau, **61**: 565-578.
- Sedgwick, A. 1873. Preface, p. i-xvii. In A Catalogue of the Collection of Cambrian and Silurian Fossils Contained in the Geological Museum of the University of Cambridge. Edited by J.W. Salter. University Press, Cambridge. 204 pp.
- Sedgwick, A., and McCoy, F. 1851-1855. A Synopsis of the Classification of the British Palaeozoic Rocks, with a Systematic Description of the British Palaeozoic Fossils in the Geological Museum of the University of Cambridge. University Press, Cambridge. 661 pp.
- Seilacher, A., and Meischner, D. 1964. Fazies-Analyse im Paläozoikum des Oslo-Gebietes. Geologische Rundschau, **54**: 596-619.
- Sennikov, V.M. 1941. On Some Siluro-Devonian Brachiopods of the Northern Altai. Sbornik Tezisev Dokladov, Nauchnii Konferentsii, Tomsk. 68 pp.
- Sepkoski, J.J. 1991. A model of onshore-offshore change in faunal diversity. Paleobiology, **17**: 58-77.
- Severgina, L.G. 1962. *Plectatrypa mediocris* sp. nov., p. 91-92. In K stratigrafii Ordovika severo-zapadno Gornogo Altaya [Ordovician Stratigraphy of Northwestern Siberia]. Edited by Z.E. Petrunina and L.G. Severgina. Materialy po Geologii Zapadnoi Sibiri, Tomskii Gosudarstvennyi Universitet, **63**: 81-93.
- Sheehan, P.M. 1982. Late Ordovician and Silurian of the eastern Great Basin, Part 4. Late Llandovery and Wenlock brachiopods. Milwaukee Public Museum Contributions Biology Geology, **50**: 1-83.

- Sheng, H.B. 1975. Silurian *Atrypella* from Guangyuan County, Sichuan. Professional Papers Paleontology Stratigraphy, **2**: 78–89.
- Shergold, J.H., and Bassett, M.G. 1970. Facies and fauna at the Wenlock/Ludlow boundary of Wenlock Edge, Shropshire. Lethaia, **3**: 113–142.
- Shergold, J.H., and Shirley, J. 1968. The faunal stratigraphy of the Ludlovian rocks between Craven Arms and Bourton, near Much Wenlock, Shropshire. Geological Journal, **6**: 119–138.
- Siehl, A. 1962. Der Greifensteinerkalk (Eiflüm, Rheinisches Schiefergebirge) und seine Brachiopodenfauna, I. Geologie, Atrypacea und Rostrospiracea. Palaeontographica **A119**: 173–221.
- Siemiradzki, J. 1906a. Monografia warstw paleozoicznych Podola. Sprawozdanie Komisji Fizyograficznej, Krakow, **32**: 87–196.
- Siemiradzki, J. 1906b. Die Paläozoischen Gebilde Podoliens. Beiträge Paläontologie Geologie Österreichs-Ungarn Orients, **19**: 213–286.
- Siveter, D.J., Owens, R.M., and Thomas, A.T. 1989. Silurian field excursions. National Museum Wales, Geological Series, **10**: 1–133.
- Smith, R.E. 1980. Lower Devonian (Lochkovian) biostratigraphy and brachiopod faunas of the Canadian arctic islands. Geological Survey of Canada Bulletin, **308**: 1–155.
- Smith, R.E., and Johnson, J.G. 1977. *Atrypella scheii* (Holtedahl) and *Atrypella phoca* (Salter). Silurian Brachiopoda. Journal of Paleontology, **51**: 350–356.
- Sowerby, G.B. 1852. A Conchological Manual. Bohn, London. 228 pp.
- Sowerby, J. 1823. The Mineral Conchology of Great Britain. Desor and Agassiz, Solothurn, Vol. 4. 148 pp. [Pl. 319–383 printed 1822.]
- Sowerby, J. de C. 1839. Organic remains [partim, 'the mollusca and conchifers by Mr. J. de C. Sowerby' vide Murchison 1839, p. 586], part 2: p. 579–712, 26 pl. In The Silurian System. Edited by R.I. Murchison. John Murray, London. 768 pp.
- Squirell, H.C., and Tucker, E.V. 1960. The geology of the Woolhope Inlier. Quarterly Journal of the Geological Society, London, **116**: 139–185.
- Squirell, H.C., and Tucker, E.V. 1967. Woolhope and Gorsley. p. 8–21. In The Silurian Inliers of the Southeastern Welsh Borderland. Edited by M.L.K. Curtis, J.D. Lawson, H.C. Squirell, E.V. Tucker, and V.G. Walmsley. Geological Association Guides, **5**: 1–32.
- Stauffer, C.R. 1930. The Devonian of California. California University Publications Geological Sciences, **19**: 81–118.
- Stel, J.H. 1978. Environment and quantitative morphology of some Silurian tabulates from Gotland. Scripta Geologica, **47**: 1–75.
- Stel, J.H., and deCoo, J.C.M. 1977. The upper Silurian Burgsvik and lower Hamra-Sundre beds. Scripta Geologica, **44**: 1–43.
- Steuber, T., and Veizer, J. 2002. Phanerozoic record of plate tectonic control of seawater chemistry and carbonate sedimentation. Geology, **30**: 1123–1126.
- Struve, W. 1966. Einige Atrypinae aus dem Silurium und Devon. Senckenbergiana Lethaea, **47**: 123–163.
- Su, Y. 1976. Brachiopoda. p. 24–326. In Paleontological Atlas of North China, Inner Mongolia, Paleozoic. Geological Publishing Company, Beijing. 502 pp.
- Su, Y. 1980. Cambrian–Devonian Brachiopoda. p. 254–327. In Paleontological Atlas of Northeast China, Paleozoic. Geological Publishing Company, Beijing. 686 pp.
- Su, Y., Rong, J., and Li, W. 1985. Brachiopods of the Bateobao Formation (Early Late Silurian) from Bateobao, Darhanmummingan Joint banner, Inner Mongolia. p. 79–102. In Silurian and Devonian Rocks and Faunas of the Bateobao Area in Darhanmummingan, Joint Banner Inner Mongolia. Edited by W. Li, J. Rong, D. Dong, D. Yang, Y. Su, and Y. Wang. People's Publishing House, Inner Mongolia. 184 pp. [N.B. publication date also sometimes cited as 1983, 1984.]
- Sundquist, B. 1982a. Wackestone petrography and bipolar orientation of cephalopods as indicators of littoral sedimentation in the Ludlovian of Gotland. Geologiska Föreningens Förhandlingar, **104**: 81–90.
- Sundquist, B. 1982b. Palaeobathymetric interpretation of wave ripple-marks in a Ludlovian grainstone of Gotland. Geologiska Föreningens Förhandlingar, **104**: 157–166.
- Temple, J.T. 1970. The Lower Llandovery Brachiopods and Trilobites from Ffridd Mathrafal, near Meifod, Montgomeryshire. Palaeontographical Society Monographs. 76 pp.
- Termier, H. 1936. Études géologiques sur le Maroc centrale et le moyen Atlas septentrional. Notes Mémoires Service Mines, Maroc, **33**: 1087–1421.
- Thomas, N.L. 1926. Brachiopods from the St. Clair Limestone, Arkansas. Denison University Science Laboratories, **24**: 385–401.
- Thomsen, E., and Baarli, G. 1982. Brachiopods of the lower Llandovery Saelabonn and Solvik formations of the Ringerike, Asker, and Oslo districts. Paleontological Contributions University Oslo, **278**: 63–78.
- Tipper, J.C. 1975. Lower Silurian animal communities — three case histories. Lethaia, **8**: 287–299.
- Tong, Z. 1984. Subdivisions of the Maoxian Group, Jiudingshan, Maowen District, Sichuan and the brachiopod faunas. Professional Papers Stratigraphy Paleontology, **11**: 61–69.
- Tsegelnyuk, P.D. 1976. Brachiopods and Stratigraphy of the Lower Paleozoic of Volyno-Podolia. Nauk Dumka, Kiev. 156 pp.
- Turek, V. 1983. Hydrodynamic conditions and the benthic community of upper Wenlockian calcareous shales in the western part of the Barrandian (Kosov quarry). Casopis Mineralogii Geologii, **28**: 245–260.
- Twenhofel, W.H. 1914. The Anticosti Island faunas. Museum Bulletin, Canada Geological Survey, **3**: 1–35.
- Twenhofel, W.H. 1916. An interpretation of the Silurian section of Gotland. In Expedition to the Baltic Provinces of Russia and Scandinavia, 1914. Edited by W.H. Twenhofel. Bulletin Museum Comparative Zoology, Harvard, **56**: 341–354.
- Twenhofel, W.H. 1928. Geology of Anticosti Island. Geological Survey of Canada Memoirs, **154**: 1–351.
- Tyazheva, A.P. 1972. Brachiopods. p. 56–141. In Korally i brachiopody podgranichnykh otlozhenii Silura i Nizhnego Devona zapadnogo sklona yuzhnogo Urala [Corals and Brachiopods in the Silurian–Lower Devonian Boundary Beds of the Eastern Slopes of the Southern Urals]. Edited by A.P. Tyazheva and R.A. Zhavoronkova. Bashkir Filial Institut Geologii Nauka, Moskva. 183 pp.
- Vail, P.R., Mitchum, R.M., and Thomson, S. 1977. Global cycles of relative changes of sea level. Memoirs American Association Petroleum Geologists, **26**: 83–97.
- Venyukov, P.N. 1899. Die Fauna der silurischen Ablagerungen des Gouvernements Podolien. Materialy Geologii Rossii, **19**: 21–266.
- Verneuil, E. de. 1848. Note sur quelques brachiopodes de l'île de Gothland. Bulletin Société Géologique France, **5**: 339–353. [With pl. 4.]
- Waagen, W.H. 1883. Salt-Range fossils. Part 1. Productus Limestone fossils, Number 4. Brachiopoda (Fascicle 2). Memoirs Geological Survey India, Palaeontologica Indica, **13**: 391–546.
- Wahlenberg, G. 1821. Petrificata telluris Svecanae examinata. Nova Acta Regiae Societatis Scientiarum Upsaliensis, **8**: 1–116.
- Wan Z. 1978a. *Dubaria rongxiensis* (sp. nov.), p. 348. In Brachiopoda. p. 284–381. Atlas of Fossils of Southwest China, Sichuan Part, Silurian–Devonian. Edited by Q. Xiu, Z. Wan, and Y. Chen. Chengdu Institute Geology Mineral resources, Chengdu. 598 pp.
- Wan Z. 1978b. "*Hircinisca*" *asiatica* Rong (MS) [sic], p. 348. In Brachiopoda. p. 284–381. Atlas of Fossils of Southwest China, Sichuan Part, Silurian–Devonian. Edited by Q. Xiu, Z. Wan, and

- Y. Chen. Chengdu Institute Geology Mineral resources, Chengdu. 598 pp.
- Wan, Z. 1982. *Spirigerina guanyingqiaoensis* Wan (sp. nov.), p. 43. In *The Silurian Stratigraphy and Paleontology of Guanyingqiao, Qijiang, Sichuan*. People's Publishing House, Chengdu. 234 pp.
- Wang, S. 1984. Brachiopods, p. 128–136. In *Paleontological Atlas of Hubei Province*. Hubei Science Technology Press, Wuhan. 812 pp.
- Wang, Y. 1956a. New species of brachiopods (i). *Scientia Sinica* **5**(1): 157–176.
- Wang, Y. 1956b. New species of brachiopods (ii). *Scientia Sinica* **5**(3): 577–601.
- Wang, Y. 1962. *Oxoplectra sinensis*, n.sp. p. 72. In *Silurian Brachiopoda*. Edited by Y. Wang and Y. Jin. p. 71–73. In *Handbook of Index Fossils in the Yangtze Valley Area*. Edited by Y. Wang et al. [32 authors]. Science Press, Beijing. 188 pp.
- Wang, Y., Jin Y., and Fang, D. 1964. Brachiopod Fossils of China. Geological Publishing House, Beijing. 777 pp.
- Wang, Y., Rong, J., and Yang, X. 1980. The genus *Atrypoides* (Brachiopoda) of Southwest China and its stratigraphic significance. *Acta Palaeontologica Sinica*, **19**: 100–117.
- Watkins, R. 1975. Silurian brachiopods in a stromatoporoid bioherm. *Lethaia*, **8**: 53–61.
- Watkins, R. 1979. Benthic community organization in the Ludlow Series of the Welsh Borderland. *Bulletin British Museum Natural History*, **31**: 175–280.
- Watkins, R. 1992. Paleocology of a low-diversity Silurian community from the Tofta beds of Gotland. *Paläontologisches Zeitschrift*, **66**: 405–413.
- Watkins, R. 2000. Silurian reef-dwelling brachiopods and their ecologic implications. *Palaios*, **15**: 112–119.
- Watkins, R., and Aithie, C.J. 1980. Carbonate shelf environments and faunal communities in the upper Brinewood Beds of the British Silurian. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **29**: 341–368.
- Watkins, R., Coorrough, P.J., and Mayer, P.S. 2000. The Silurian *Dicelostia* communities: temporal stability within an ecologic Evolutionary Unit. *Palaeogeography Palaeoclimatology Palaeoecology*, **162**: 225–237.
- Watts, N.R. 1988. Carbonate particulate sedimentation and facies within the Lower Silurian Högklint patch reefs of Gotland, Sweden. *Sedimentary Geology*, **59**: 93–113.
- Watts, N.R., and Riding, R. 2000. Growth of rigid, high-relief patch reefs, Mid-Silurian, Gotland. *Sedimentology*, **47**: 979–994.
- Wenzel, B., and Joachimski, M.M. 1996. Carbon and oxygen isotopic composition of Silurian brachiopods (Gotland/Sweden): palaeoceanographic implications. *Palaeogeography Palaeoclimatology Palaeoecology*, **122**: 143–166.
- Whiteaves, J.F. 1904. Preliminary list of some fossils from the Silurian (Upper Silurian) rocks of the Ekwan River, and Sutton Mill lakes, Keewatin, collected by D.B. Dowling in 1901, with descriptions of such species as appear to be new. *Geological Survey of Canada Annual Report*, **14**: 38–59.
- Williams, A. 1951. Llandovery brachiopods from Wales with special reference to the Llandovery district. *Quarterly Journal of the Geological Society, London*, **107**: 85–136.
- Williams, A., Brunton, C.H.C., and Carlson, S.J. (Editors). 2002. *Treatise on Invertebrate Paleontology, Part H, Brachiopoda (revised), Vol. 4: Rhynchonelliformea (part)*. Geological Society of America and University of Kansas Press, Lawrence, KS. pp. 921–1688.
- Worsley, D., and Broadhurst, F.W. 1975. An environmental study of Silurian atrypid communities from southern Norway. *Lethaia*, **8**: 271–286.
- Xu, H. 1979a. *Zanclorhyncha* Xu gen. nov. p. 96–97. In *Brachiopoda*, p. 60–217. *Paleontological Atlas of Northwest China (Qinghai)*, Vol. 1. Edited by Y. Jin, S. Ye, H. Xu, and D. Sun. Geological Publishing House, Beijing. 393 pp.
- Xu, H. 1979b. *Qilianotryma* Xu gen. nov. p. 97–98. In *Brachiopoda*, p. 60–217. *Paleontological Atlas of Northwest China (Qinghai)*, Vol. 1. Edited by Y. Jin, S. Ye, H. Xu, and D. Sun. Geological Publishing House, Beijing. 393 pp.
- Xu, H. 1979c. *Zygospira* (Sulcatospira) Xu subgen. nov. p. 109–110. In *Brachiopoda*, p. 60–217. *Paleontological Atlas of Northwest China (Qinghai)*, Vol. 1. Edited by Y. Jin, S. Ye, H. Xu, and D. Sun. Geological Publishing House, Beijing. 393 pp.
- Xu, H. 1979d. Brachiopods from the Tangxian Formation (Devonian) in Nandan, Guangxi. *Acta Palaeontologica Sinica*, **18**: 362–380.
- Yadrenkina, A.G. 1978. Brachiopods, p. 69–90. In *Ordovik Sibirskoi Platformy, Opornye razrezy Verkhnego Ordovika (Biostratigrafiya i fauna) [Ordovician of the Siberian Platform, Key Sections of the Upper Ordovician (Biostratigraphy and Fauna)]*. Edited by T.A. Moskalenko, A.G. Yadrenkina, V.S. Semenova, and A.M. Yaroshinskaya. *Trudy Sibirskii Nauchno-issledovatel'skii Institut Geologii Geofiziki*, **340**: 1–138.
- Zadoroshnaya, N.M., Osadchaya, D.V., and Novoselova, L.N. 1982. *Semka v raionakh razvitiya otlozhenii s organogennymi postroikami [Growth and Regional Development of Strata and Their Organogenic Deposits]*. Nedra, Leningrad. 328 pp.
- Zeng, Q. 1987. Brachiopoda, p. 209–537. In *Biostratigraphy of the Yangtze Gorge area*, Vol. 2. Edited by X. Wang. Geological Publishing House. 589 pp.
- Zeng, Q., Liu, Y., Wan, J., Pei, F., Yan, G., Zhang, Q., and Du, F. 1993. Succession and ecology of brachiopod faunas across the Ordovician–Silurian boundary south of the eastern Qinling mountains. *Acta Palaeontologica Sinica*, **32**: 372–383.
- Zhang, Y. 1981. Early Devonian brachiopods from Zhushilenghairhan region, western Neimongol. *Acta Palaeontologica Sinica*, **20**: 383–392.
- Ziegler, A.M. 1964. The Malvern line. *Geological Magazine*, **101**: 467–469.
- Ziegler, A.M. 1965. Silurian marine communities and their environmental significance. *Nature*, **207**: 270–272.
- Ziegler, A.M., Cocks, L.R.M., and McKerrow, W.S. 1968. The Silurian transgression of the Welsh Borderland. *Palaeontology*, **11**: 736–782.
- Ziegler, A.M., Rickards, R.B., and McKerrow, W.S. 1974. Correlation of the Silurian rocks of the British Isles. *Geological Society of America Special Paper*, **154**: 1–154.

Appendix

Gotland atypid localities

[ordered by alphabetic location]

Numbers for localities in brackets at end of locality data as 'SW'. For remaining localities consult Allekvia master list of Lennart Jeppsson, Lund University, and Laufeld, 1974b.

Balsklint 1. 1.5 km WNW of harbour at Lickershamn. Upper Visby beds, below resistant Höglint, 7J Färösund SV 14800:59360 [SW84].

Bankvät 2. Bedding plane outcrop near SE coast, ca. 300 m S of 'b' in Bankvät, ca. 1.3 km NNE of point at Flunting; thin, hard limestone of Eke beds, 5I Hoburgsvägen NO 34250:57450 [SW101].

Batels 4. Ditch excavation, west side of road Dalhem-Kräklingbo, 200 m S of intersect road to Ganthem, east side of road between Hartviks and Tule; Klinteberg Fm., 6J Roma NV 79640:64940 [SW71].

Bengts 1. North side of roadcut, road Östergarn-Hertvik, ca. 2 km E of Östergarn church; Hemse beds, unit C, with *Atrypa* sp., 6J Roma SO ca. 70290:85500 [SW26].

Blahäll 1 [Laufeld locality]. Coastal bluff section; collections from shaly horizons below more resistant upper beds, type locality *Oglupes muldea* from Mulde Maris, lower units, 6I Visby SO 56750:41800 [SW16].

Bodudd 1. Beach outcrops on N side Bodudd peninsula; *Atrypa alata* in oncolitic Eke beds, 5I Hoburgsvägen NO 29570:44700 [SW126].

Bogeklint 1 [Laufeld locality]. Circa 1.2 km S of intersect Gothem-Boge road and Slite-Bäl road, SW of town of Slite, raukar locality around small reefs; Slite beds (unit G), 6J Roma NV 77200:97800 [SW10].

Djaupevik East 1. East coast, temporary beach exposure [access by removing algae from bedrock], at SW side of narrow bay 'Djaupevik', 200 m SW 'D' of 'Djaupevik', ca. 1 km E of Lilla Hammars [ca. 6 km ESE of Kräklingbo]; <1 m soft-weathering shales, ripple-marked micrites, Hemse beds, unit 'A' or 'B', rich in rhynchonellids, with rare *Atrypoides sulcata*, 6J Roma SO ca. 74810:79420 [SW24 = SW75].

Djaupeviksudden 2 [Laufeld, 1974b]. Coastal outcrop at point on S side of Djaupevik, ca. 800 m N of coastal outcrop Träske 2; brachiopods collected in stromatoporoid biostrome, Hemse beds unit A[?], 6J Roma SO 74790:79600 [SW74].

Djaupeviksudden 4 [Bergman, 1989]. Beach outcrop at N end of embayment, ca. 300 m N of Djaupevik East 1 [SW24]; Hemse beds, unit A[?], 6J Roma NV 75080:79690 [SW76].

Djupvik 1 [= ca. Djupvik 1 of Laufeld, 1974b]. More southerly coastal exposures of bluffs, collection of *Oglupes muldea* in levels between favositid horizon below and heliolitid horizon above, for ca. 200 m along strike, Mulde Marl, 6I Visby SO 55700:55900:40800-41100 [SW88].

Djupviksvägen 1 [Ramsköld, 1984]. Drainage ditch outcrop, ca. 300 m SE of Djaupevik, ca. 200 m due S of 'k' in Djaupevik on map, on N side of road leading into field [type locality *Glossia djaupevik*]; soft shales of Mulde facies, 6I Visby SO 55730:41660 [SW44].

Färsviken 2. Low beach outcrop exposed at low tide ca. 100 m NW along bay, around small spit of outcrop, shaly layer very rich in *Didymothyris didyma*, and probable type locality of this species [as seen in Riksmuseet localities], Hemse beds, low unit C, 6J Roma SO 72780:84750 [SW92].

Färsviken 3. Low beach outcrop at low tide, at deep end of Färsviken Bay, first outcrop going N on west side of bay, probable alternate type locality of *Atrypa reticularis*, syringopores with gastropods, rare brachs; shaly partings of lower Hemse unit C,

6J Roma SO 72720:84720 [this is the only locality which yields common specimens identical to the Linnaeus species type material]. May be known under other locality names, e.g., Hammarudden (in Hede, 1960), Hammaren (in Hede, 1960), etc., that appear at other localities in the area [SW91].

Föllingbo 5. Ditch outcrop on north roadside, ca. 250 m NW of Föllingbo; Slite beds, lower units, 6J Roma NV 88540:53560 [SW58].

Gane 1 [Laufeld locality]. Excavations for telephone poles along road, ca. 3 km E of Bäl; Slite beds, Slite Marl (see Martinsson, p. 50), 6J Roma NV 95200:71600 [coordinates slightly different from Laufeld, 1974b] [SW11].

Gannarveskär 1. Beach outcrop of Slite sandstone, ca. 1.9 km SW of Mulde, collection of *Plagiorthyncha dormitzeri* from 10 cm thick sandstone bed, 6I Visby SO 60960:42350 [SW120].

Gannes 3. Old quarry near Östergarn; loose Hemse beds, unit C, with broken *Atrypoides primum*, 6J Roma SO 70410:82580 [SW51].

Gannes 4. Ditch outcrop along S side of road, ca. 700 m W of church Östergarn; Hemse unit C, with common well-preserved whole *Atrypoides primum* [this may have been the source stratum for 'Östergarn' type locality of *A. primum* shells], 6J Roma SO 70500:82800 [SW52 = SW90].

Garnudden 5. Shoreline exposures; soft-weathering shales with abundant *Atrypoides sulcata*, in stromatoporoid biostrome, Hemse beds unit A, 6J Roma NV 75500:79400 [SW36].

Garnudden 6. Beach outcrop locality at 'H' of Hammarudden (lower left side of H), 950 m due SW of Garnudden triangulation point, stromatoporoid biostrome with *Atrypoides sulcata* in abundance; Hemse beds, unit A, 6J Roma NV 75620:79850 [SW77a].

Garnudden 7. Beach outcrop on NW side of point flanking S side of Garnudden Bay, 720 m due SW of triangulation point Garnudden; Hemse beds unit A, stratigraphically below SW77a, 6J Roma NV 75410:79800 [SW77b].

Garnudden 8. Beach outcrop at embayment notch, 200 m coast S of Garnudden 6, with favositids; Hemse beds, unit A, 6J Roma NV 75380:79780 [SW77c].

Garnudden 9. Shoreline exposure, 150 m S of Garnudden 6; shaly pockets between stromatoporoid biostrome, with abundant *Atrypoides sulcata*, Hemse beds, unit A, 6J Roma NV 75550:79450 [SW37].

Garnudden 10. Coastal outcrop ca. 800 m SSE of Garnudden, directly S of pillbox; thin shaly layers between micrites of Hemse beds, unit A, with abundant *Rhytidorhachis*, 6J Roma NV/NO ca. 75500:79820 [SW25].

Gnåsvärd 1 [Laufeld, 1974b; see Hede, 1960]. Collections on N and E side of harbour dredged from harbour excavations; Lower Visby shales [type locality *Gotatrypa hedei*], 6I Visby NO 77700:38400 [SW8].

Gothemshammar 5 [Laufeld, 1974b]. Low Klinteberg beds, ca. 3-4 m above base Halla, rhynchonellid beds, 6J Roma NV 90300:79470 [SW49].

Gothemshammar 6. Beach outcrops with stromatoporoids; Halla beds, unit C, 6J Roma NV 91200:78600 [SW19].

Grogarns 4. Beach outcrop in situ, ca. 800 m ESE of 's' in Grogarns, ca. 1.2 km S of Grogarnshuvud triangulation point [see van Hoepen's localities *Atrypoides primum*]; Hemse beds, unit C, 6J Roma SO 71900:85800 [SW21].

Grogarns 5. Beach outcrop 300 m S of Grogarns 4, 1.5 km S of point at Grogarnshuvud; Hemse beds, unit C, 6J Roma SO 71610:85950 [SW22].

Grunnsudden 2. Shaly to micritic beach outcrops on small point, on N side of Skarnvik Bay, facing Garnudden, ca. 500 m SW of

- 'G' in Grunnsudden; this is shown as uppermost Klinteberg Limestone, but is 'Hemse facies', with common small chonetids, ribbed *Conchidium*, 6J Roma NO 77190:78520 [SW115].
- Grunnsudden 3.** Beach outcrop opposite side of small embayment, 200 m N of Grunnsudden 2, *Conchidium*, small *Acerularia*, rhynchonellids; upper Klinteberg Limestone in Hemse shaly-micritic facies, 6J Roma NO 77320:78540 [SW116].
- Gustavsvik 1.** Crumbly weathering soft shales along shoreline, ca. 100 m N of side road going up slope [Hedström, 1910, locality]; upper part of Lower Visby shales, 6I Visby NO ca. 95700:49500 [SW2].
- Gutevägen 3** [Laufeld locality]. Quarry on SW outside of Visby city walls, adjacent to Shell Oil tanks (on access road to city bypass), ca. 300 m due N of 'Kopparsvik' [ca. 90 m S, 110 m W of Laufeld, 1974b, locality]; Höglint beds, 6I Visby NO 92400:47800 [SW9].
- Hagrummet 4.** Roadcut road Kräklingbo – Dalhem Romakloster, 800 m NNW parish church Kräklingbo intersect Hwy 146, 300 m NW of old Dahlem road intersect, ca. 480 m W of Hagrummet; reef in Klinteberg Limestone, 6J Roma SV 73320:74100 [SW50].
- Hägsarve 6.** Ditch outcrop, W side of road to Snoder, ca. 400 m S of Hägsarve farm; shaly Hemse facies, unit B?, with small *Atrypa*, 5I Hoburgen NO 48850:44100 [SW103].
- Hägsarve 7.** Drainage ditch on cross road next to wooded area, E side of road to Snoder, 700 m S of Hägsarve farm; shales with fauna different from Hägsarve 1, stratigraphically higher in lower Hemse, 5I Hoburgen NO 48550:44350 [SW104].
- Hägsarve 8.** Field and ditch locality ca. 300 m NNW of Hägsarve farm, 150 m W of road to Snoder; Hemse facies with Klinteberg corals, stromatoporoids, 5I Hoburgen NO 49420:43800 [SW122].
- Hallsarve 1** [close to Laufeld, 1974b, locality]. Inland bluff on W side of curved road; upper Hemse beds, 3–4 m below Eke contact, 6J Roma SV 54160:70950 [SW57].
- Hallshuk 5.** Low coastal bluffs, 130 m S of light, below 'h' of Hallshuk; Upper Visby beds, 7J Färösund NV 25900:74570 [SW83].
- Hammarudden 2.** Beach outcrop on Hammaren peninsula, west side facing island of Storgunn, 900 m N of Vassmunds; thin, 2–3 cm brown soft shale with nests of *Didymothyris*, in bedded micrites, Hemse beds, lower unit 'C', 6J Roma SO 72890:83960 [SW127].
- Hammarudden 3.** Coastal outcrop on peninsula W side of Färsviken [designated type locality for *Atrypa reticularis*], micrites with shaly partings on beach, syringopores, gastropods, rare brachiopods; Hemse beds, 'unit C', 6J Roma SO 73170:84550 [SW70, SW93].
- Hemse 1** [see Fredholm, 1988a, b]. Temporary sewer excavation running E–W in SE part of town; Hemse beds, unit C, 5J Hemse NV ca. 48300:55500–55600 [SW27].
- Hien 1.** Beach outcrop on N coast of Stora Karlsö [see Hede, 1927b, fig. 19, for photo of locality], biostromal facies with large solitary rugosans *Dokophyllum*, *Plectatrypa parimbricata*, in uppermost Slite beds (or Mulde?), 6I Visby SO 53670:30210 [SW108].
- Histilles 1.** Beach outcrop, ca. 1.2 km NE of second 's' in Histilles; thinly bedded micrites exposing ca. 1.5–2 m of lower Hemse beds, high unit 'A' or low 'B', 6J Roma SO 75380:79600 [SW78].
- Hoburgen 2.** Upper outcrops along cliff face; in situ collection from restricted type locality *Spirigerina quinquecostata*, in single nest of small patch reef facing west, Hamra beds, 5I Hoburgen SO 12960:41340 [SW35].
- Holmhällar 3.** Shoreline outcrop on W side of bay facing Heligholmen island; Sundre reefs, 5I Hoburgen SO 14180:50750 [SW56].
- Hörsne 3** [Laufeld, 1974b, data]. Drainage ditch section, Halla beds, unit B, 6J Roma NV ca. 84900:67200 [SW18].
- Husryggen 1** [close to Laufeld, 1974b, localities Kättelviken, but not determinable as any of these]. Bluffs W of coastal road; brachiopods in lower Hamra beds, from 2–3 m above Burgsvik Sandstone, 5J Hemse SV 15260:42680 [SW55].
- Ireviken 1.** Coastal bluffs SW of Irevik, collection 1.5–2.5 m above high tide, with halysitid biostromes and small patch reefs with brachiopods; Lower Visby shales, 7J Färösund NV 16600:64280 [SW80].
- Ireviken 2.** Shoreline outcrops at base of bluffs on SW side of Irevik Bay, Hede, 1960, locality 13 (see also Kartbladet Kappelshamn, Munthe et al., 1933); collection from upper part of Lower Visby shales, 7J Färösund ca. 16400:64680 [SW6].
- Ireviken 3.** Beach outcrop at 'S' in Snipan, collection directly below Höglint Fm.; Upper Visby beds, 7J Färösund NV 16720:63900 [SW82].
- Ireviken 5.** Coastal outcrops in halysitid reefs with brachiopods, phaceloid rugosans, and 'Omphyma', but further to west in next bay, around point; Lower Visby shales, 7J Färösund NV 16670:64090 [SW81].
- Kappelshamn 1** [ca. 125 m from Laufeld site]. Old quarry N of Kappelshamn; Höglint beds, unit B, 7J Färösund SO 18600:76500 [SW42].
- Kattlunds 1.** Excavation for large cesspool, on S side of barn, adjacent to road, ca. 2 km S of Grötlingbo; Eke beds with oncolites (*Rothpletzella* balls, identical lithology to beds around Näs), 5I Hoburgen NO 34720:53540 [SW29].
- Klinte 7.** Drainage ditch Hwy 141, ca. 600 m E of Klinte 10, SE of Klintehamn; Slite beds, with large *Pentamerus*, 6I Visby SO 64030:44530 [SW95a].
- Klinte 10.** Intersect south bypass for Klintehamn going NE, drainage ditch; shaly Slite beds, with brachiopods, 6I Visby SO 64080:43950 [SW95].
- Klinteberget 2.** Loose collections from top to middle part of section next to quarry; low–mid Klinteberg beds, =? possible type locality of *Spirigerina marginalis*, but ca. 350 m S of classic Klinteberget locality [Jeppsson, personal communication], 6I Visby SO ca. 64000:46200 [SW17].
- Kneippbyn 3.** Coastal cliffs exposed in cliff face, ca. 50 m S of Skjutfält barrier; Upper Visby shales, particularly around small bioherms, with rich peri-reefal brachiopod fauna, 6I Visby NO ca. 89800–90000:45700–45800 [SW7].
- Kodings 2.** Ditch excavation; shales with abundant *Dayia*, rare *Atrypa sowerbyi*, Hemse beds, unit C, 5J Hemse NV 48100:56180 [SW28].
- Kronvald 2.** Drainage ditch along road Kronvald to Burge, ca. 5.5 km W of Eksta; Mulde Marl, high, 6I Visby SO 52700:38870 [SW89].
- Lambskvie 1.** Directly at 'v' of Lambskvie; Hemse beds, unit C, with athyrids, rhynch. type locality of *Rhytidorhachis didonta*, 6J Roma SO ca. 74200:77200 [SW20].
- Lau Backar 1.** Loose weathering collections from bedding plane surfaces; Eke beds, *Rhizophyllum* Lst., brachiopods, corals, 6J Roma SV ca. 54900:70800 [SW23].
- Lekarve 1.** Small temporary excavations just S of house or farm marked 'Lekarve', ca. 400 m S of Valbytte 1 of Laufeld, 1974b, E side of road along seashore, directly at parking area N side, ca. 1.3 km S of Västergarn; blue–grey 'Slite' marls, 6I Visby SO 69580:40730 [SW13].
- Lerberget 4.** Stora Karlsö, coastal outcrops N of slumped blocks on beach, lower bluffs with softer weathering shaly units (see foreground, below photo in Hede, 1927a, fig. 20), brachiopod collection from immediately below the coral biostromes at this level [type locality *Plectatrypa parimbricata*], upper Slite beds, 6I Visby SO 53470:29800 [SW111].
- Liekershamn 1.** Collection from marker bed [below bentonite of Laufeld, 1974b; colln. ca. 260 m NW of Laufeld, 1974b, original locality]; Upper Visby shales adjacent to small patch reefs with *Xanthea lamellosa*, *Oglupes*, etc., 7J Färösund SV, ca. 15000:60200 [SW5].

- Lickershamn 4.** Bluffs 400 m NW of pier at Lickershamn; small patch reefs of upper 'Lower' [or ?upper] Visby beds. 7J Färösund SV 14720:60510 [SW86].
- Lilla Snögrinde 4** [Frykman, 1985]. Small quarry ca. 1 km SE of Klinte church; Klinteberg Lst., collection in upper 2 m exposed, 6I Visby SO 63750:47150 [SW113].
- Lindarve 1.** Ditch outcrop on S side of road, 1.6 km W of N-S road Hägsarve-Snoder; shaly Hemse facies with small *Atrypa harknessi*, 5I Hoburgen NO 48860:42470 [SW102].
- Ljugarn 1** [part of Laufeld, 1974b; Watkins, 1975]. Shoreline outcrop, around raised, small patch reef ca. 100 m W of 'L' in Ljugarn, collected from upper part of one small patch reef, as nests between stromatoporoids; reefal facies Hemse beds, unit E?, with *Atrypa hemsea*, 6J Roma SO 59150:75320 [SW38].
- Loggarve 2.** Extensive roadcut ca. 2 km NE of Klinte road to Hejde; Klinteberg Lst., low units, above contact Mulde Marl, 6I Visby SO 66000:48270 [SW53].
- Lushalet 1.** Stora Karlsö, outcrops ca. 80 m N of Lerberget 4 beach collection, directly below tourist lookout and lighthouse, base of cliffs where beach vanishes (Hede, 1927a, fig. 20); collection from Rasenriff coral biostrome, ?upper Slite, 6I Visby SO 53550:29800 [SW112].
- Mulde Tegelbruk 1** [Hede, 1960, locality 30]. Loose dumped material on spill heaps, common *Oglupes muldea*; Mulde Marls, 6I Visby SO 61300:43870 [SW46].
- Mulde Tegelbruk 2.** Loose collections at shrimp pond excavations [and housing construction 1995], S of Mulde, 700 m N of stone boat monument [= equivalent to old Mulde Tegelbruk dump sites, but slightly S of older collections]; Mulde Marl with abundant brachs, *Oglupes muldea*; 6I Visby SO 61200:43800 [SW96].
- Näs 2.** Soft-weathering exposures ca. 1 km ENE of Näs, 200 m W of main road to Havdhem; Eke beds, with *Atrypa alata*, in field on S side of side road to Näs, 5I Hoburgen NO 49450:34950 [SW30].
- Näs 3.** Circa 200 m S of Näs 2, ditch excavation on E side of road, 500 m SW Näs church; oncolitic *Rothpletzella* balls covering *Atrypa alata*, Eke beds, 5I Hoburgen NO, ca. 33830:48530 [SW31].
- Nyhamn 4** [very close to Bergman, 1989, locality]. Trench cut into beach for boat landing, adjacent to bunker; Lower Visby beds, 7J Färösund SV 06950:55200 [SW59].
- Nyhamn 6.** Circa 100 m S of Nyhamn 3, harbour dug for boats between erratics; clays in Lower Visby beds, 7J Färösund SV 06900:55200 [SW130].
- Petesvik 1A.** Shoreline outcrops directly 0–50 m S of fence coming to shore edge, and fishing huts, on bed plane surfaces (Schmidt, 1859; van Hoepen, 1910, locality), exposing brachiopods *Atrypa purchisoni*, *Cyrtia*, etc. (see also later localities Sandskallen, SW100 and SW100a); Hemse western facies [see also Jaanusson, 1986, as Petesvik 1], 5I Hemse NV 42950:42550 [SW54].
- Ramroir 1** [Ramraur in Hede, 1927a, name changed in newer maps]. Stora Karlsö W coast, ca. 300 m N of Stormasen, 400 m S of lighthouse, bedding plane beach outcrop collections along base of bluffs, in biostromal coral dominated layers, ?upper Slite, 6I Visby SO 53200:29780 [SW109].
- Ramroir 2.** Circa 200 m N of Ramroir 1, just S of protruding slump blocks on beach; stratigraphic collection in shales about 1–2 m above Ramroir 1 levels, upper Slite beds?, 6I Visby SO 53350:29820 [SW110].
- Raudklint 1.** First point and cliffs 800 m N of Stenkyrkehuk; lower part of Upper Visby beds, 7J Färösund SV 14100:58470 [SW85].
- Rönklint 2.** Beach outcrops N Lummelunda, at low tide, N of resistant bed; soft blue shales of Lower Visby beds, 7J Färösund SV 11900:57020 [SW43].
- Rudvier 1** [Ramsköld, 1986]. Old quarry, ca. 3 km N of Ljugarn, collection from soft shales with *Spiriferina costata*, in mid-level of quarry, below stromatoporoid biostrome; Hemse beds, units D–E, below reefal level, 6J Roma SV 62600:73100–73250 [SW79].
- Sandskallen 2.** North margin of bay, shoreline bedding plane outcrops along road from Sandskallen; low Hemse beds, with Petesvik fauna included, rare *Septatrypa petesvika*, *Atrypa purchisoni*, 5I Hoburgen NO 43280:42190 [SW100].
- Sandskallen 3.** As above, first bedding plane exposures adjacent to wooded area on road from coastal road to Sandskallen, ca. 300 m W of SW100 (Sandskallen 2), low Hemse beds, shaly facies, 5I Hoburgen NO 43320:41950 [SW100a].
- Särvät 1.** Ditch locality at canal intersecting road from Rodarve to Nisse, ca. 200 m NW of junction road to Alsvik on coast, 5J Hemse NV 39200:44000 [SW123].
- Sigvalde 2** [Laufeld, 1974b]. Inland cliff, near Sigvaldetrask, ca. 90 m E of Laufeld site; reefal Hemse facies, units D–E, *Atrypa poidea hemsea*, 6J Roma SV 60700:64500 [SW33].
- Skäls 2.** Field locality at modern wind turbine, 4 km SSW of Olsvenne; oncolitic Eke beds with rich *Atrypa alata* fauna, 5I Hoburgen NO 29000:45700 [SW125].
- Skäls Café 1.** Field locality with many loose brachiopods weathered out (many oncolitic coated *Atrypa alata*), in field directly opposite Skäls Café and handicraft barn, E side of road, ca. 200 m NW of old windmill; Eke oncolitic beds, 5I Hoburgen NO 32880:48210 [SW124].
- Skälsö 1** [Larson, 1979, locality]. Shoreline outcrop ca. 4 km W of Väskinde church, 150 m NE of pillbox, 250 m NNE ditch and road. Lower Visby beds, 6J Roma NV 99580:52060.
- Slitebrottet 1.** Quarry, outcrops alongside quarry wall entrance ramp; Slite Marls, 7J Färösund SO/NO 02330:78320 [SW12].
- Smissarve 3.** Road drainage ditch outcrop 2.3 km SW of Slite parish, 1.1 km SW along road to Sandskallen from #140 main road, with abundant heliolitids, rare brachs; Hemse facies, very low, unit A, 5I Hoburgen NO 45470:44760 [SW97].
- Smissarve 4.** Drainage ditches 1.2 km SW of Smissarve 3, along same road to Sandskallen; Hemse facies with *Atrypa purchisoni* (fauna matches Petesvik locality), low unit A, 5I Hoburgen NO 44770:43750 [SW98].
- Smissarvestrand 1.** Small exposures on bed plane surfaces next to seashore; sparsely fossiliferous low levels of Hemse [Petesvik] facies with *Atrypa purchisoni*, 5I Hoburgen NO 44000:41750 [SW99].
- Snäckgårdsbaden 1.** Roadcut leading up to escarpment; collections in soft-weathering Upper Visby shales, with *Gotatrypa*, *Plectatrypa abbreviata*, *Dicoelasma*, associated with small patch reefs as inter-reef strata, 6J Roma NV ca. 96400:50660 [SW4].
- Snäckgårdsbaden 3.** Shoreline locality, temporary outcrop of shales near end of small road along shore (below 'd' of 'Friluftsbad'); shales with small *Gotatrypa*, *Plectatrypa abbreviata*, small rhynchonellids, small solitary corals, halysitids; Lower Visby beds or base of Upper Visby beds, 6J Roma NV ca. 96900:50750 [SW3].
- Snäckvik 2.** Beach locality almost at last 'k' of Snäckvik, exposing about 1 m of oncolites; Eke beds, with *Atrypa alata*, 5I Hoburgen SO 22000:45680 [SW94].
- Snoder 2.** South side of canal, loose excavations; Hemse shales, western facies, with *Atrypa purchisoni*, 5I Hoburgen NO ca. 47900:44800 [SW32].
- Stavsklint 2** [in Tofta Skjutfält]. Collections along strike for ca. 200 m SW of, and to, Stavsklint main cliff base, from uppermost part of cliffs below Höglint resistant weather units; Upper Visby beds, 6I Visby NO 83600–85000:39250–39350 [SW47].
- Stora Banne 3** [ca. 80 m from Laufeld, 1974b, locality]. Quarry, with collection from lower shelly bed; Slite beds, 'unit G', 7J Färösund SO 13400:76900 [SW41].
- Stora Banne 4** [ca. 170 m from Laufeld, 1974b, locality]. North of Simunds, old roadcut with small reefs, ca. 2 km N of Lärbro; Slite beds, unit G, 7J Färösund SO 12800:77200 [SW40].
- Stora Myre 1** [Laufeld, 1974b, locality]. Field exposure NW of house, 1530 m due S of Martebo church, ca. 350 m W of southernmost house along main road at Stora Myre; Slite beds, unit

- D, soft-weathering argillaceous micrites, 7J Färösund SV 04200:60100 [SW39].
- Storugns 1.** Large active quarry on west side of Kappelpshamn Bay, 300 m NNW of triangulation point Storugns on map, on S side of quarry, 7J Färösund SO 15780:78920 [SW87].
- Stutsviken 2.** Beach outcrop of reefal carbonates, ca. 100 m W of fishing huts, with rich brachiopod fauna, cf. *Xanthea lamellosa*, *Endreia*, etc. [possibly = famous locality of 'Lansa'], N coast of Färö island, Stutsviken Bay, lower Slite beds, 7J Färösund SO 26520:92870 [SW106].
- Stutsviken 3.** Patch reefs ca. 100 m W of Stutsviken 2, beach outcrop; lower reefal Slite beds, 7J Färösund SO 26580:92820 [SW107].
- Sudervik 2.** Low beach exposures, 1.6 km S of intersect Kronvald fiskeläge [ca. 70 m S of Jeppsson locality] with *Ogluipes muldea* and *Glassia djauvika*; Mulde Marls, 6I Visby SO 51420:38050 [SW45].
- Svarvare 3** [Larsson, 1979]. Ditch on E side of main road Klintehamn–Fröjel, Slite beds with *Glassia djauvika*, 6I Visby SO 63380:44120 [SW121].
- Tänglings 4.** Road outcrop ca. 2 km S of Etelhem along road to Lye; reefal Hemse beds, upper units D–E, 6J Roma SV 58600:62820 [SW34].
- Tjälderholm 1.** Beach outcrop in and around small reef, exposed at low tide ca. 80 m from small pier [not Tjeldersholm 1 of Laufeld, 1974b, which includes strata above the reef; not Tjelders of Jaanusson (1986), which is inland]; high Slite beds, type locality *Gutnia capitula*, 6J Roma NV 93630:77400 [SW48].
- Träske 2.** Bulldozed coastal beach outcrop, at end of road from Träske to coast; soft-weathering shales in Hemse beds, unit A, with stromatoporoids, brachiopods, 6J Roma SO 74230:79180 [SW73].
- Trojeborg 1.** Roadside bluff section (Hede, 1960, locality 4); Högklint reef margin outcrop, 6I Visby NO ca. 94600:49300 [SW1].
- Tule 2** [see Laufeld, 1974b, Tule 1]. East side of road between Hartviks and Tule, ca. 300 m S of Tule, opposite farm; Klinteberg beds, unit E, 6J Roma NV 77780:66680 [SW72].
- Valar 5.** Old quarry [slipstenbrott], ca. 3 km W of Burgsvik; oolitic–pisolitic, oncolitic Hamra beds overlying Burgsvik Sandstone, 5I Hoburgen NO 25420:47220 [SW105].
- Valbytte 6.** Roadside outcrops almost following shoreline, Västergarn–Klintehamn road, E side road, ca. 2 km S of Västergarn centre; Slite beds, soft shales, 6I Visby SO 68580:40920 [SW14].
- Valbytte 7.** Excavation ca. 100 m S of Valbytte 6, along same road following shoreline; Slite shales, 6I Visby SO 68480:40920 [SW15].
- Ygne 2** [extension of Laufeld, 1974b, locality]. Coastal cliff section ca. 1.5 km S of Högklint cliff; collection from lower 1.5 m exposed, in Upper Visby shale at beach level, 4–5 m below patch reef horizon, 6I Visby NO 87360:42060 [SW114].

Plates 1–29

Plate 1

Fig. A, a–l. *Zygatrypa exigua* (Lindström, 1861)

Lower Visby Fm., Ygne Mbr., late Llandovery – ?Högklint Fm., early Wenlock.

a–d. Paralectotype Br13690, elongate specimen, Häftingsklint, ?Högklint Formation.

e–h. Elongate paratype Br136906, Rönklint 1, Lower Visby beds.

i–l. Wide paralectotype Br136907, Rönklint 1, all $\times 5$.

Fig. B, a–j. Alexander (1949) collection of '*Atrypa reticularis*'

a–e. *Atrypa (Atrypa) sowerbyi* Alexander 1949, holotype A11626, Sedgley, Staffordshire, Sedgley Limestone, middle Ludlow.

f–j. Holotype A11625 of *Atrypa (Atrypa) sedgwicki* Alexander 1949, Craven Arms, Shropshire, 'Aymestry Limestone', early Ludlow [= *Atrypa reticularis* Linnaeus 1758]; $\times 2$.

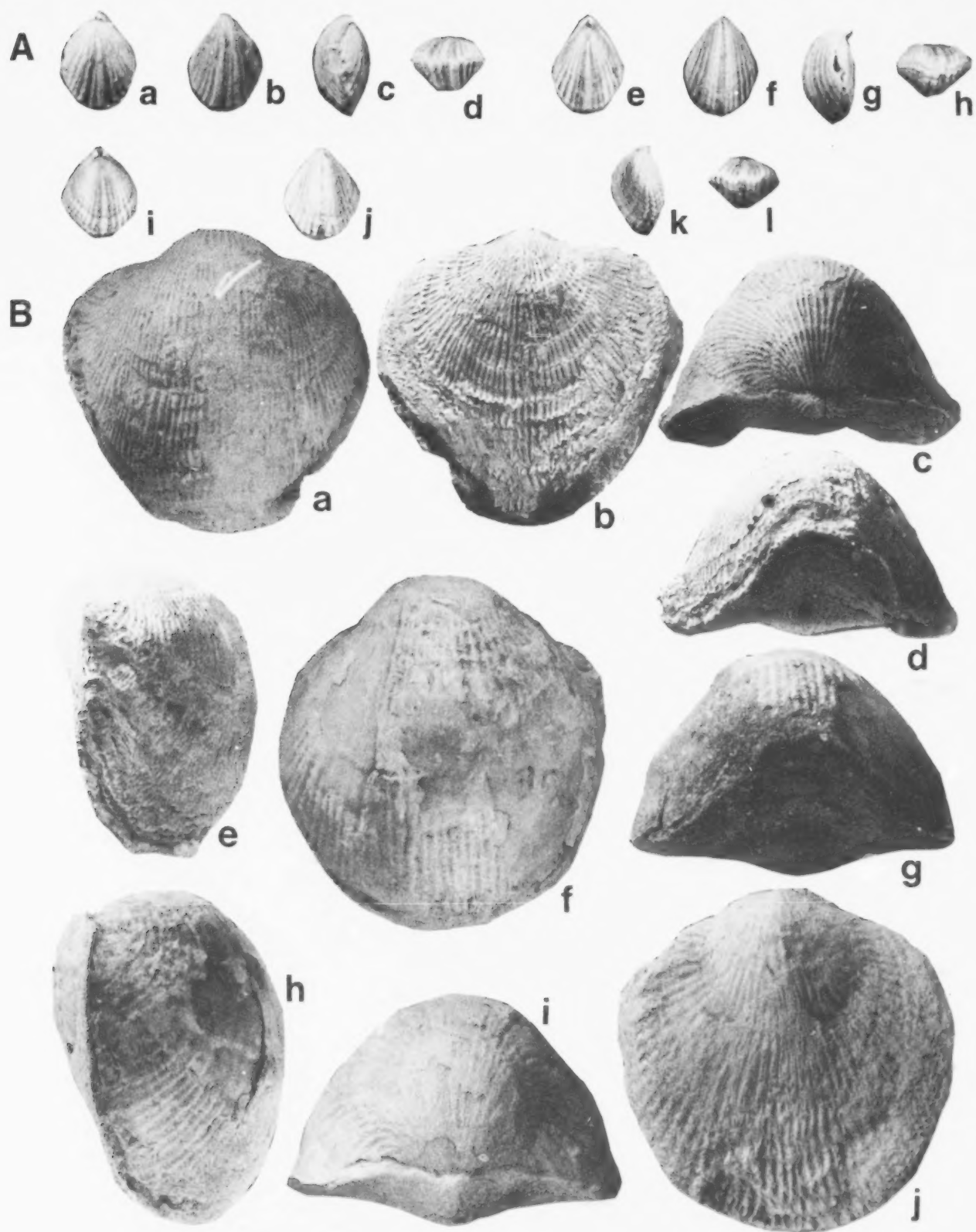


Plate 2

Figs. a–o. *Atrypa (Atrypa) reticularis* Linnaeus, 1758

'Hammarudden', E coast Gotland, lower Hemse beds, unit C, *scanicus* Zone, Gorstian, early Ludlow.

a–e. Lectotype Linnaeus collection, 'Gotland' [photo P. Copper].

f–i. Medium-sized shell, Br104039.

j–l. Large shell, hypotype Br104655.

m. Loose ventral valve, Br115446.

n. Loose vv with partially preserved frill, Br115445.

o. Loose vv, Br115447; all from 'Hammarudden', probable locus typicus, $\times 2$.

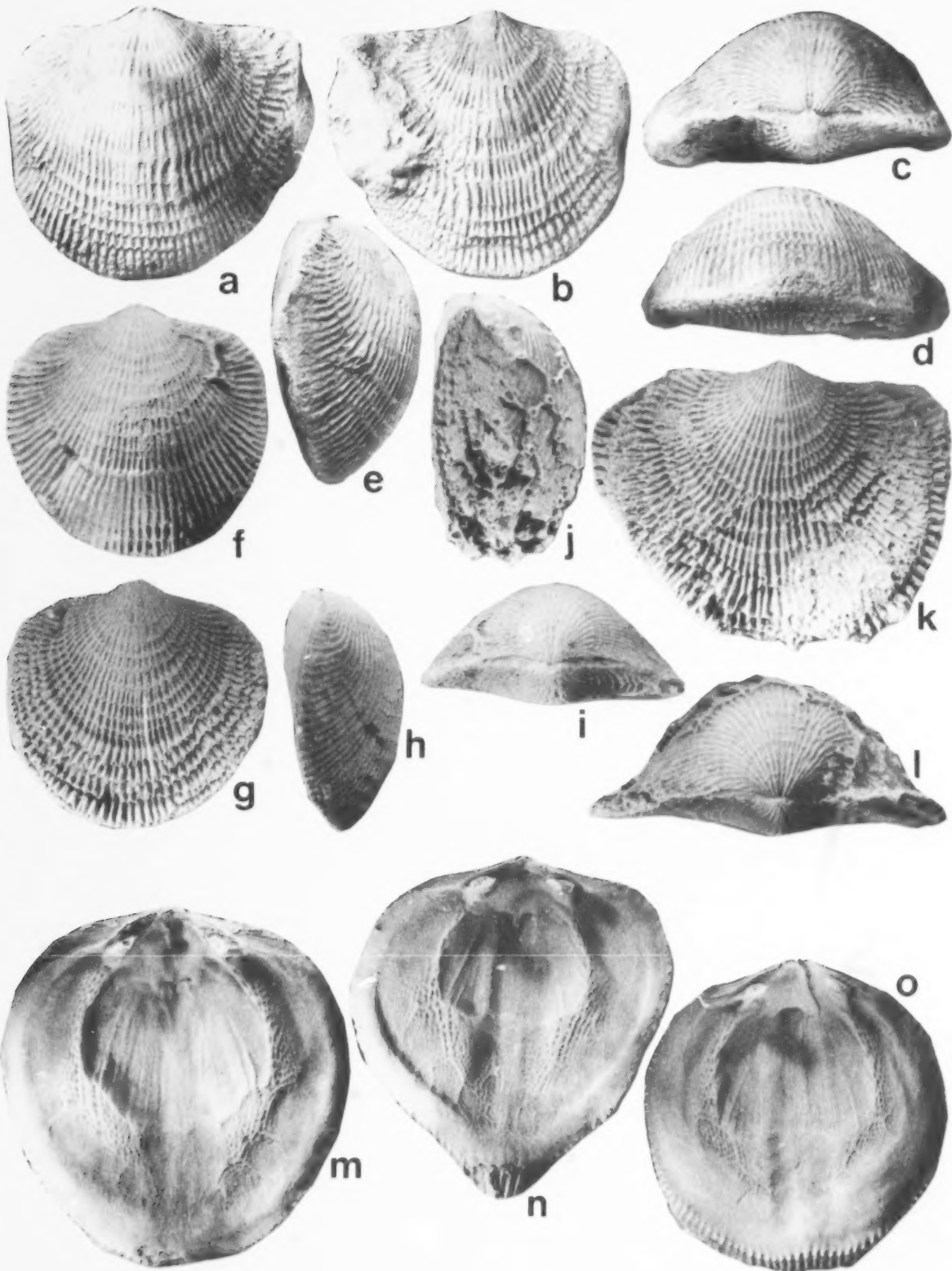


Plate 3

Figs. a–v. *Atrypa (Atrypa) sowerbyi* Alexander, 1949

Upper Hemse beds, middle Ludlow, Gotland.

a–e. Typical specimen, Br134642.

f–j. Wider shell with frill, Br106572, Bengts.

k. Adult shell, Br43229, with single frill projecting from dorsal valve, ovoid perforations at breaking edge, Yanges Kanal.

l–p. Neanic shell, Br106570.

q. Dorsal valve removed, displaying spiralia, Br106573.

r. Internal of dv, Br106547.

s, t. Oblique and normal view of ventral valve interior, Br106575, Hemse Ost.

u. Ventral valve, Br106574, Hemse Ost.

v. Ventral valve broken to show spiralia, Br134619, Näs; all $\times 2$.

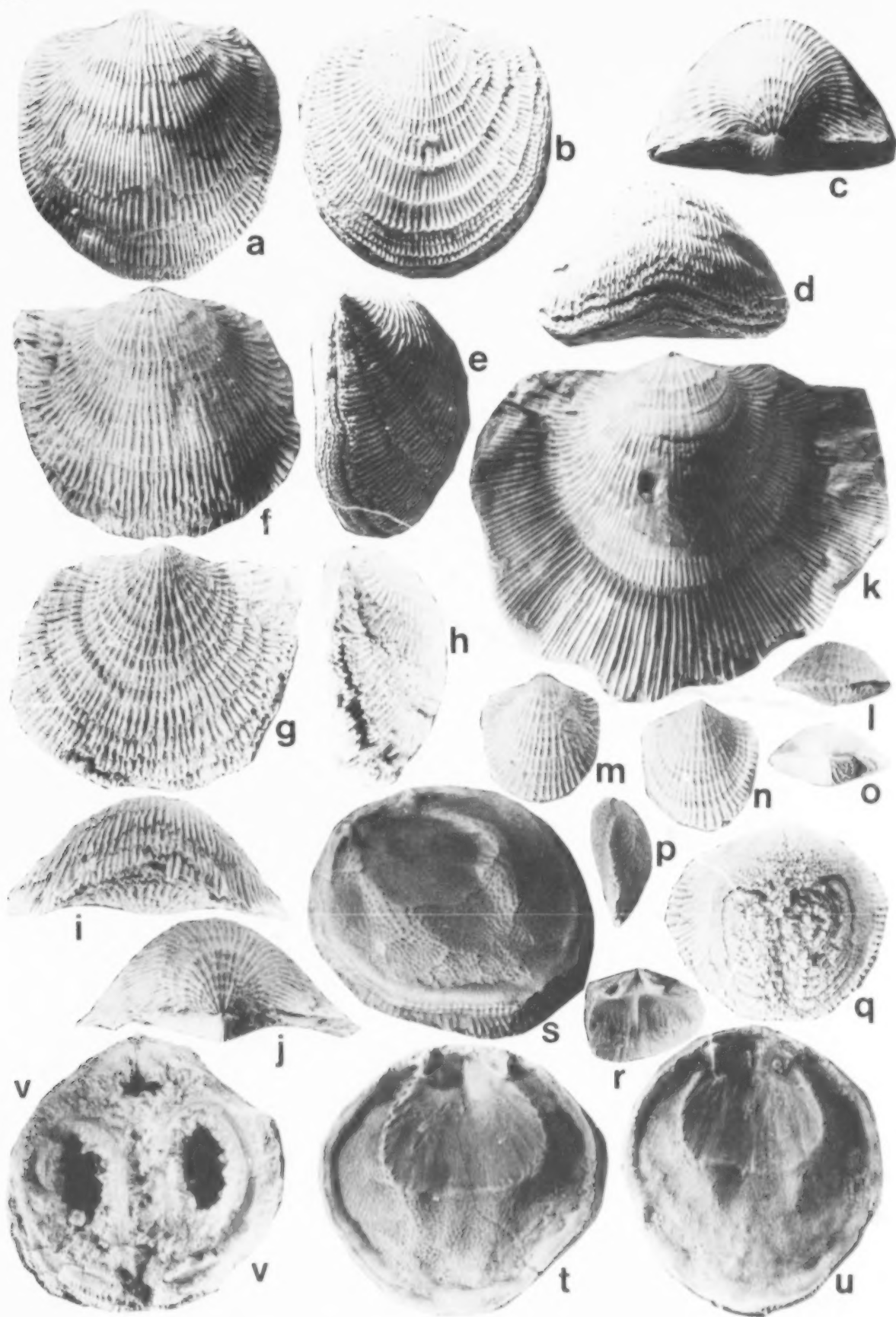


Plate 4

Fig. A, a–l. *Atrypa (Atrypa) gotha* n. sp.

Stavsklint, uppermost Upper Visby beds, lower Wenlock.

a–c. Holotype Br106590, specimen showing strong rib flattening and smoothing on the growth lamellae.

d–h. Large specimen, paratype Br106591, with coarse, flattened ribs on growth lamellae [N.B. nearly smooth growth lamellae overlie normal ribs underneath at anterior commissure].

i–l. Paratype Br106589, smaller specimen; all $\times 2$.

Fig. B, a, b. *Atrypa (Atrypa) plana* Sowerby, 1839

'Tynewidd', Wales, Wenlock Shale, ?early Wenlock.

a. Lectotype GSM6611, ventral valve lectotype on left side, with a dorsal valve on right side.

b. Another portion of slab GSM6611 with part of a ventral valve.

Fig. C, a–o. *Atrypa (Atrypa) harknessi* Alexander, 1949

Bradlow, middle–upper Wenlock Shale, middle Wenlock.

a–e. Holotype Br11621, Alexander colln.

f–j. Large shell with frill, hypotype, Br106588, Robbjäns.

k–o. Average-sized shell, Br106587, Robbjäns; all $\times 2$.

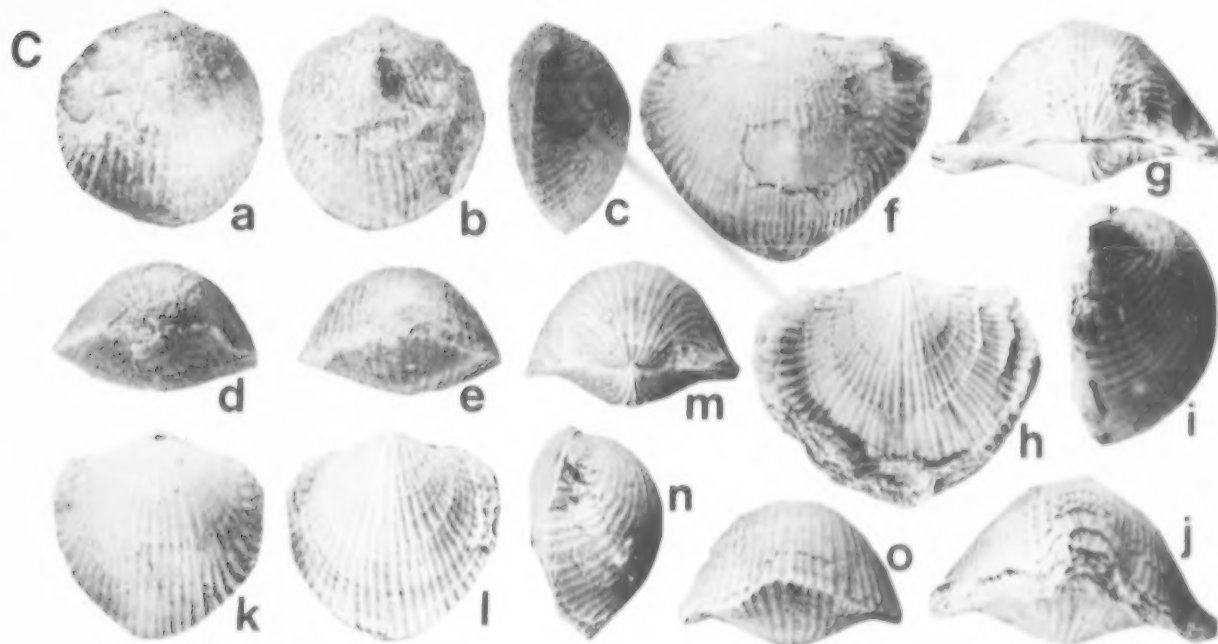
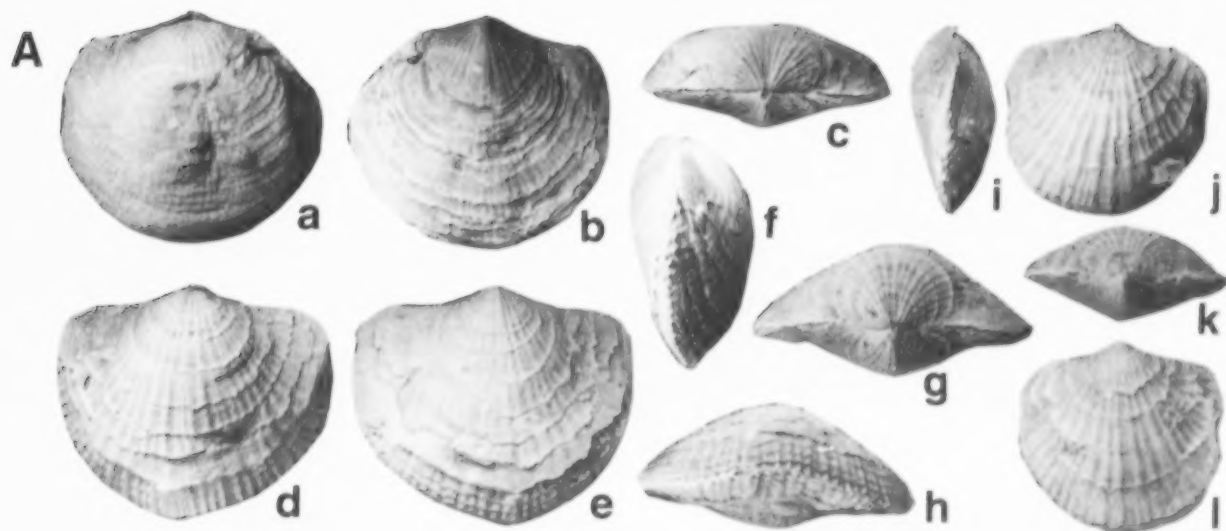


Plate 5

Figs. a-m. *Atrypa (Atrypa) slitea* n. sp.

Middle Slite Formation, middle Wenlock.

a-e. Holotype Br103384, with frill, Hejdeby canal.

f. Ventral valve, paratype Br107908, Martille.

g-k. Immature specimen, paratype Br48857, Storvede.

l-m. Medium-sized specimen, paratype Br103459, Suderbys; all x2.

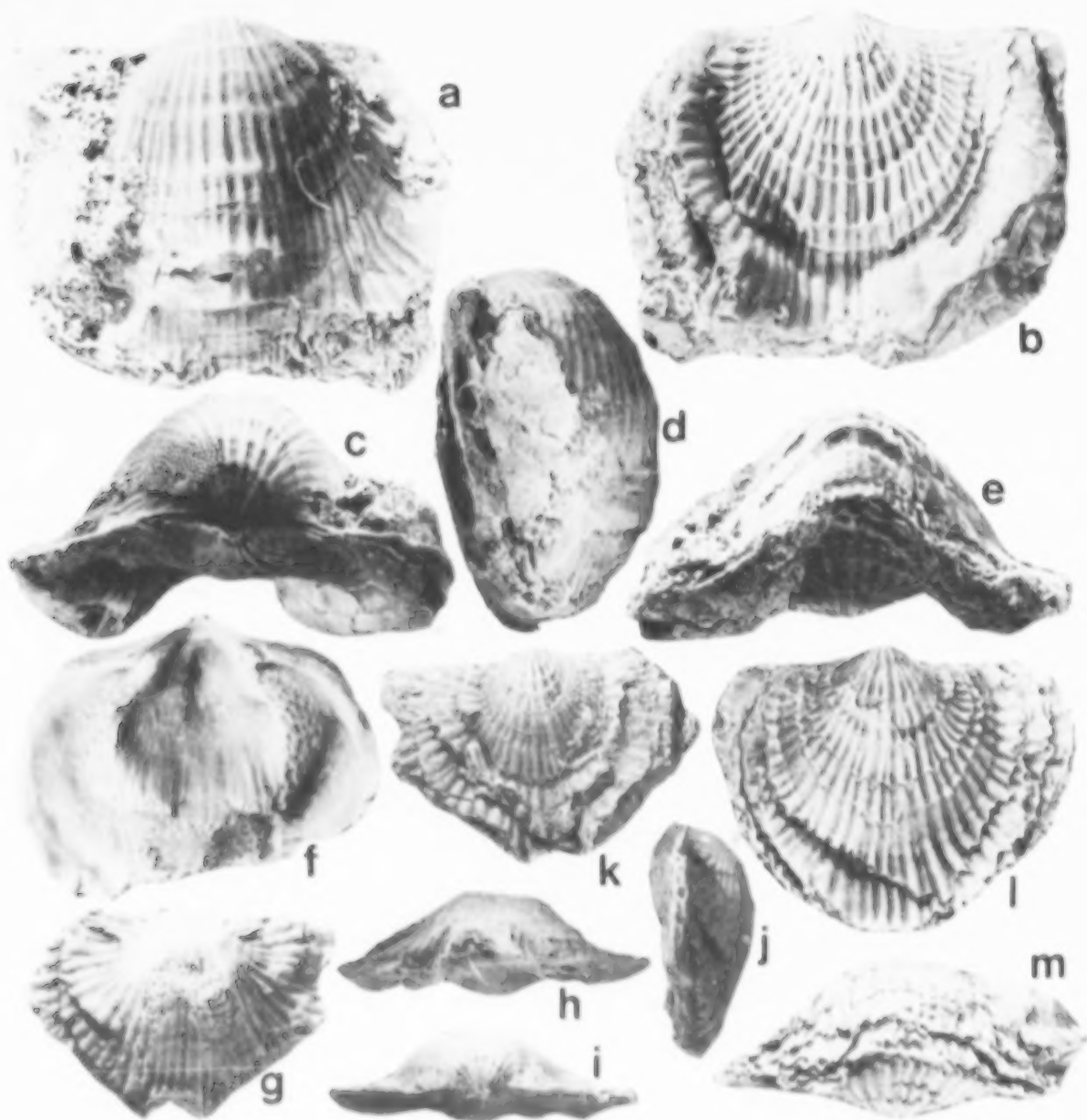


Plate 6

Fig. A, a–g. *Atrypa (Atrypa) harknessi* Alexander, 1949

Lowermost Hemse Formation, SW facies, early Ludlow, Hagsarve 2.

a–d. Wider shell with frill, Br106527.

e–g. Larger, more dorsibiconvex shell, Br106528; $\times 2$.

Fig. B, a–k. *Atrypa (Atrypa) alata* Hisinger, 1831

Eke Formation, middle Ludlow.

a–d. Paralectotype Br2030, large shell with frills, Lindström collection.

e, f. Paralectotype, Br2048, medium-sized shell, Lindström collection.

g–k. Neanic shell, hypotype Br124721, from post-Lindström collection, 'Näskyrka'; all $\times 2$.

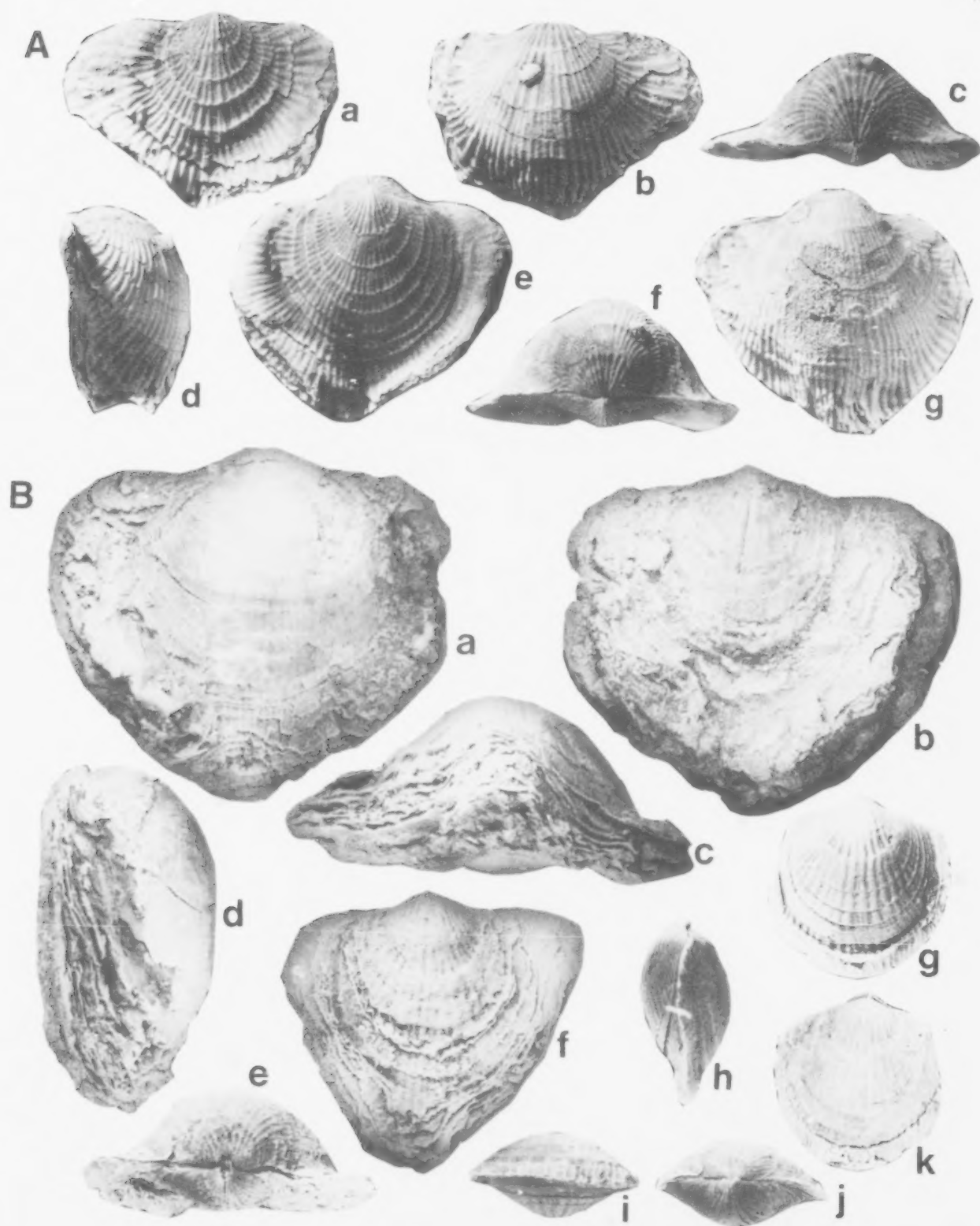


Plate 7

Figs. a-q. *Atrypa (Atrypa) affinis* (Sowerby, 1822)

Wenlock Limestone or Klinteberg Formation, late Wenlockian.

a-d. Lectotype GS4151, Sowerby collection, 'Dudley'.

e-h. Paralectotype GS4149.

i-m. Hypotype Br107929, large specimen, 'Klinteberg'.

n-q. Hypotype BB55381, lowermost Elton beds (early Ludlow), Shadwell Quarry, Wenlock Edge.

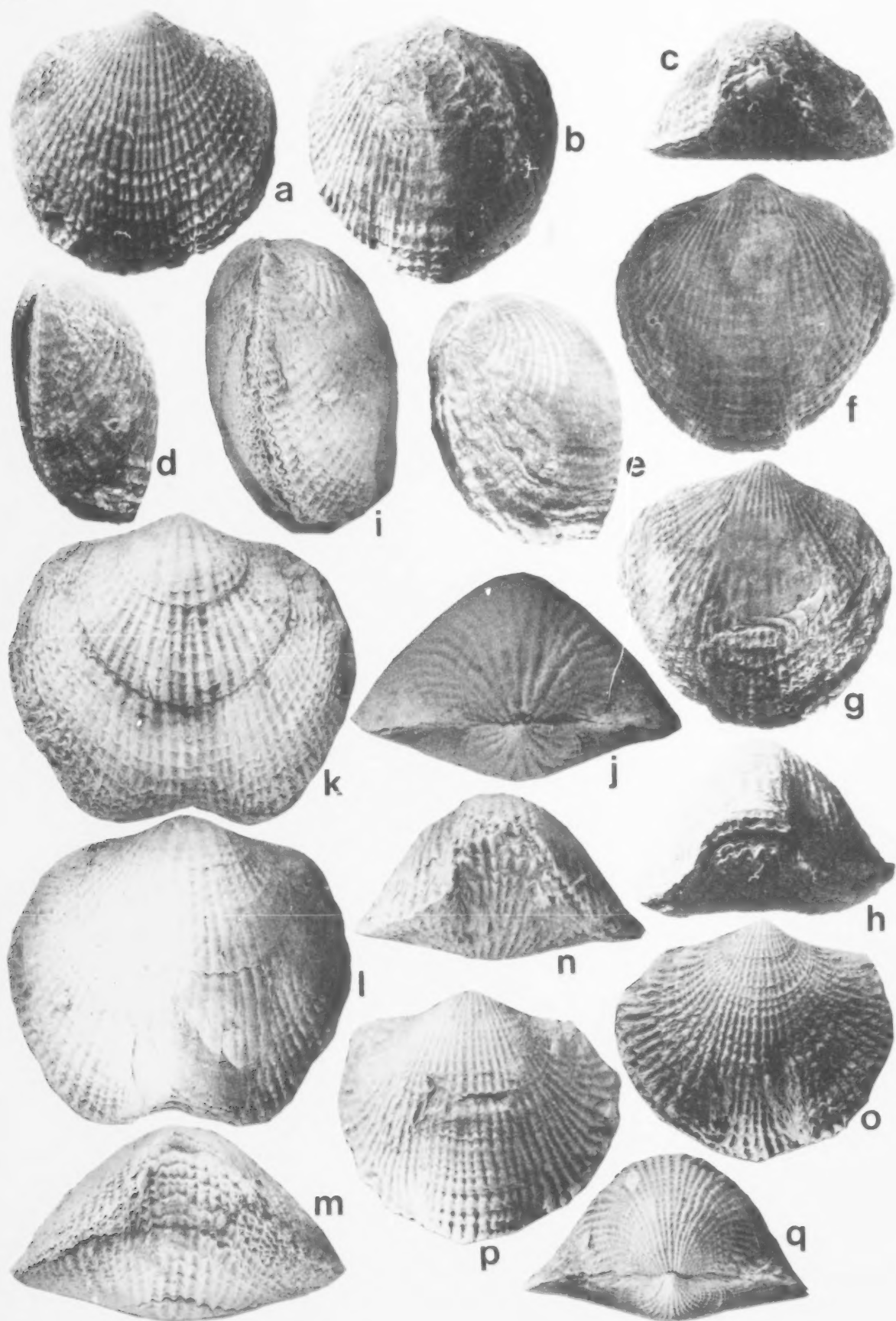


Plate 8

Figs. a–v. *Atrypa (Atrypa) lapworthi* Alexander, 1949

Elton beds, lowermost Ludlow.

a–e. Hypotype BB55371, large specimen.

f–j. Immature shell, hypotype BB55369.

k–o. Large shell with bryozoan epibiont on dorsal valve, hypotype BB55372.

p–q. Intermediate shell size, hypotype BB55370.

[a–q.] All from Shadwell Quarry, 1–3 m above Wenlock Lst. contact].

r–v. Holotype A11623, Alexander collection, Nacklestone; all $\times 2$.

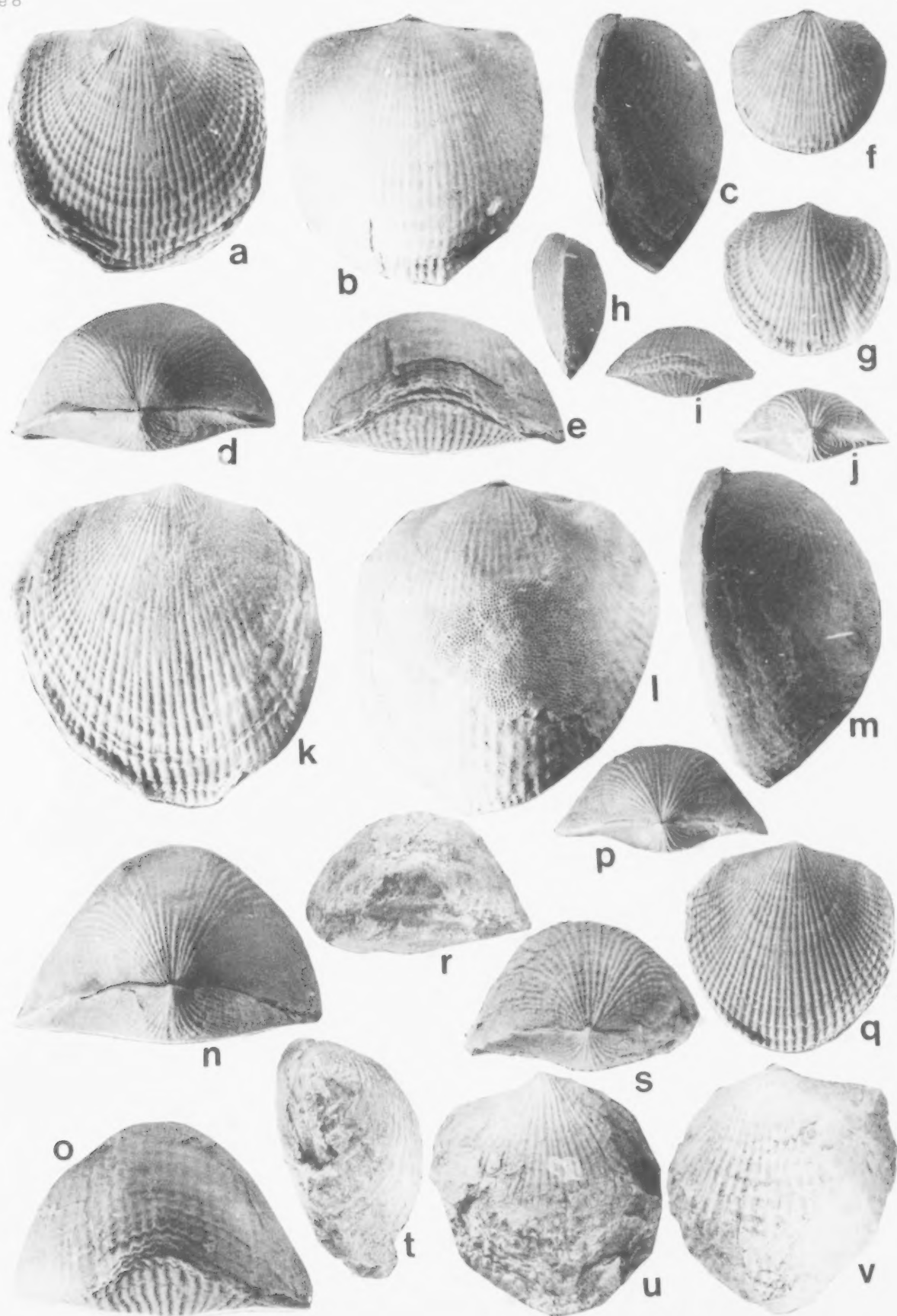


Plate 9

Fig. A, a–z, za. *Atrypa (Atrypa) murchisoni* Alexander, 1949

'Lower Ludlow Shales' (a–e, u–z), Elton Fm. (f–k), lower Hemse Fm. (k–o), Gorstian, Ludlow.

a–e. Holotype A11624, Alexander colln.

f–j. Hypotype BB55378, Shadwell Quarry.

k–o. Partly decorticated shell, hypotype Br104081, Petesvik 1.

p–t. Neanic shell, hypotype BB55377, Shadwell Quarry.

u. Broken dv, paratype A12341.

v. Smaller whole dv, paratype A12334.

w. Large dv, paratype A12343.

x, y. Broken vv, paratype A12336.

z. Broken vv, paratype A12342.

a–e, u–z, za. Ledbury, type locality; all x2.

Fig. B, a–e. *Gotatrypa orbicularis* Sowerby, 1839

Telychian, Llandovery.

a–e. Lectotype GSMGsd6073, a biconvex shell, Gorllwyn-Fach, Wales; lateral view reversed, with vv right; anterior, posterior views reversed, with vv upwards (photos courtesy of D.E. White); x2.

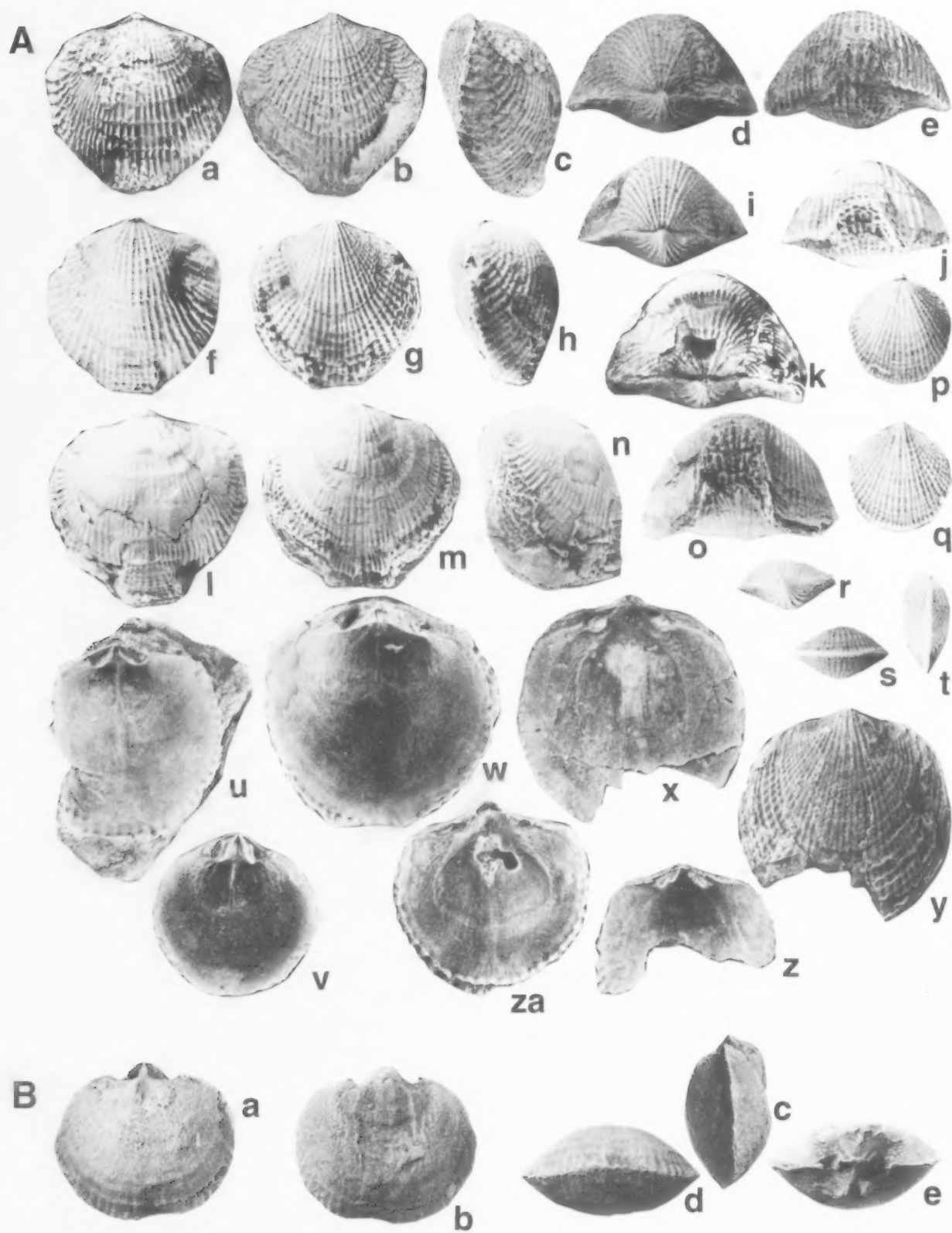


Plate 10

Fig. A, a–i. *Atrypa (Atrypa) woodwardi* Alexander, 1949

Ludfordian, late Ludlow, Shropshire, and Hamra Fm., Gotland.

a–d. Alexander holotype A11629, Dinchope, Shropshire, upper Ludlow Shales.

e, f. Typical adult shell, Br42318, Hamra beds, Burgsvik.

g, h. Br42319, loose ventral valve showing large diductor scars, Hamra Fm., Burgsvik.

i–l. Specimen with straighter hinge, Br42317, Hamra Fm., Burgsvik, late Ludlow; all $\times 2$.

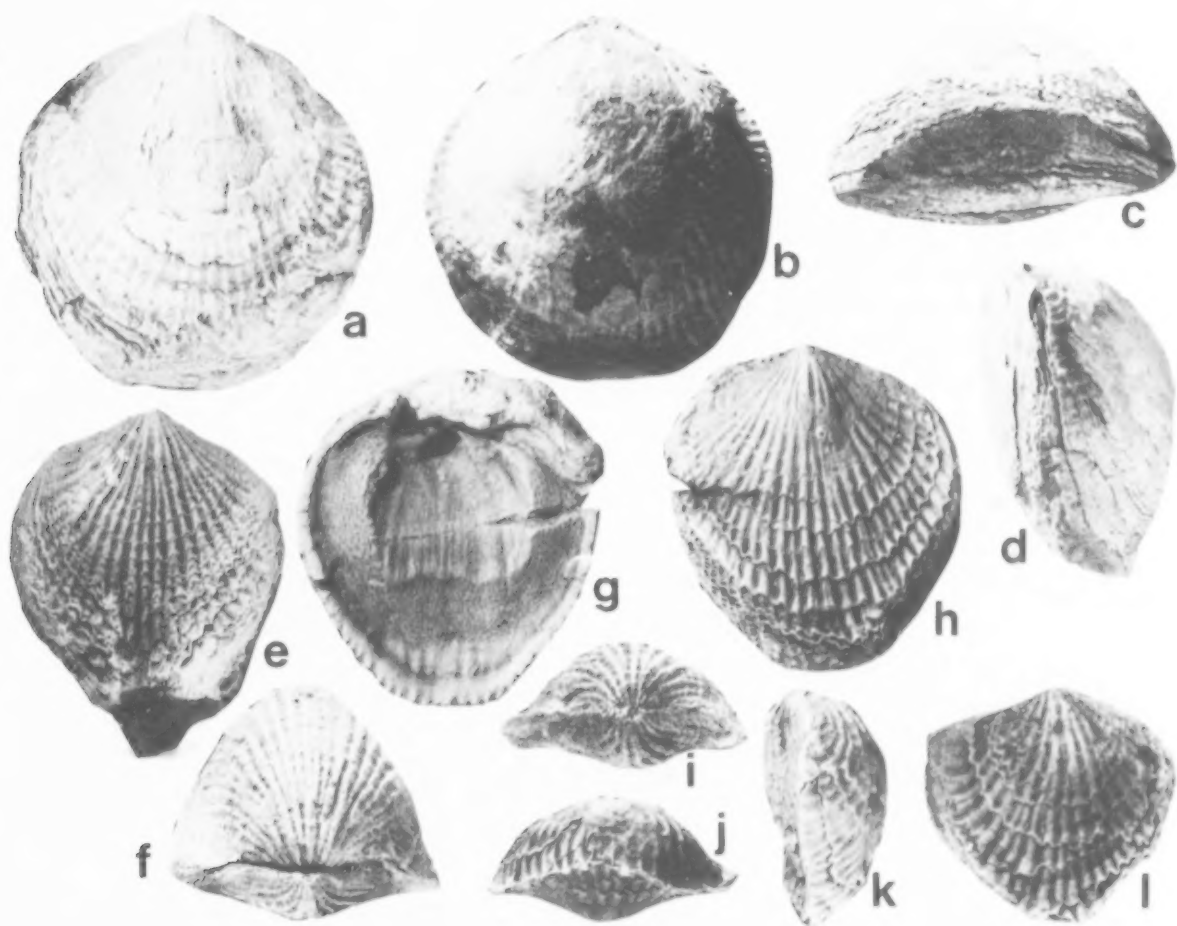
Fig. B, a–i. *Gotatrypa hedei* Struve, 1966

Talludden, Lower Visby beds, Ygne Mbr., Telychian.

a–e. Adult large shell, hypotype Br104111, showing fine ribs.

f–i. Hypotype Br104112, both $\times 2$.

A



B

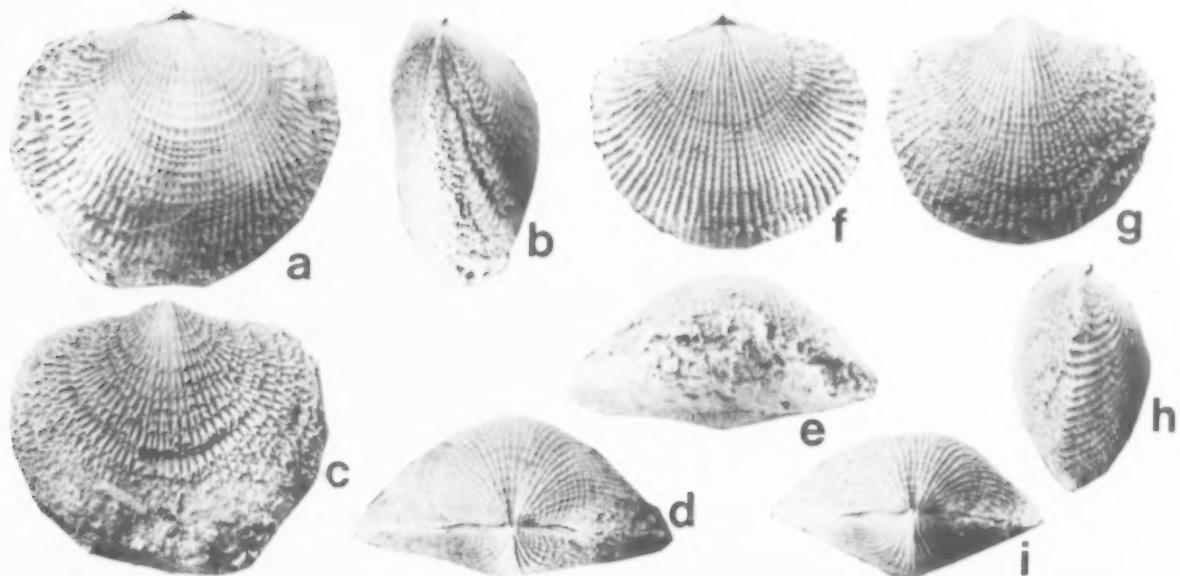


Plate 11

Fig. A, j-s. *Gotatrypa hedei* Struve, 1966

'Visby', Lower Visby beds, Ygne Mbr., Telychian.

j-n. Small shell, Br104113.

o. Ventral valve, with weakly incised scars, Br108023, Visby.

p. Ventral valve with strongly developed muscle scars, Br108034, Visby.

q. Ventral valve Br108029, Visby.

r. Ventral valve Br108022, Visby.

s. Br108024, Visby; all $\times 2$, except o, r, s, $\times 3$.

Fig. B, a-s. *Oglupes davidsoni* (Alexander, 1949)

Homerian, Wenlock.

a-e. Holotype, A11620, 'Storridge, Woolhope Limestone', ca. middle Wenlock.

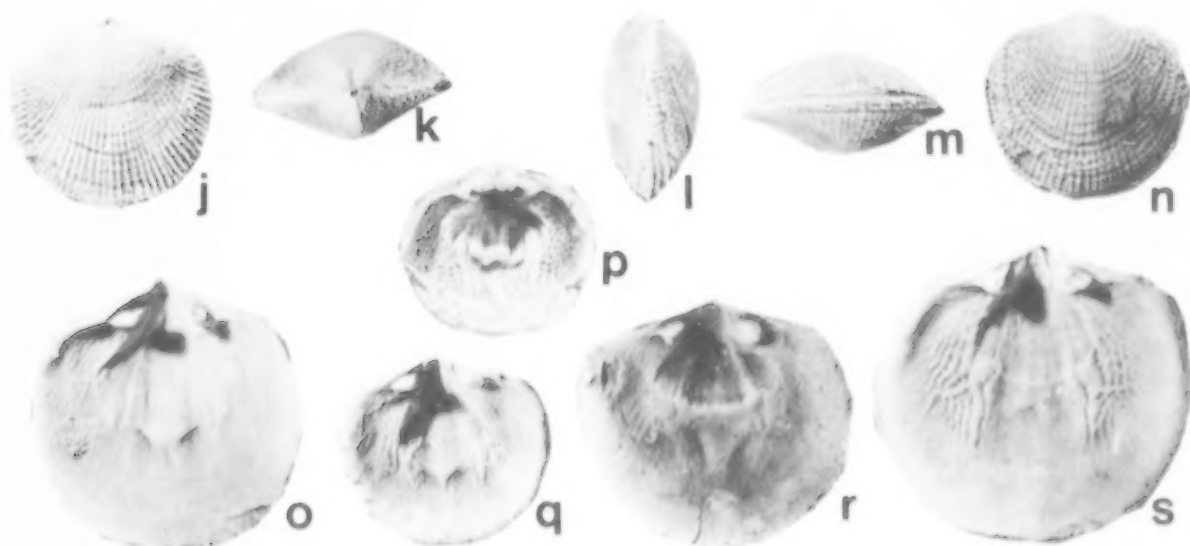
f-j. Mature specimen with typical short frill, hypotype Br106533, Lerberget, Stora Karlsö Island.

k-n. Neanic shell, Br103945, Lerberget.

o-r. Larger specimen with weak anterior fold, Br103974, Lerberget.

s. Detail of short frill on dorsal valve, Br106533, Lerberget, Slite beds, middle Wenlock.

A



B

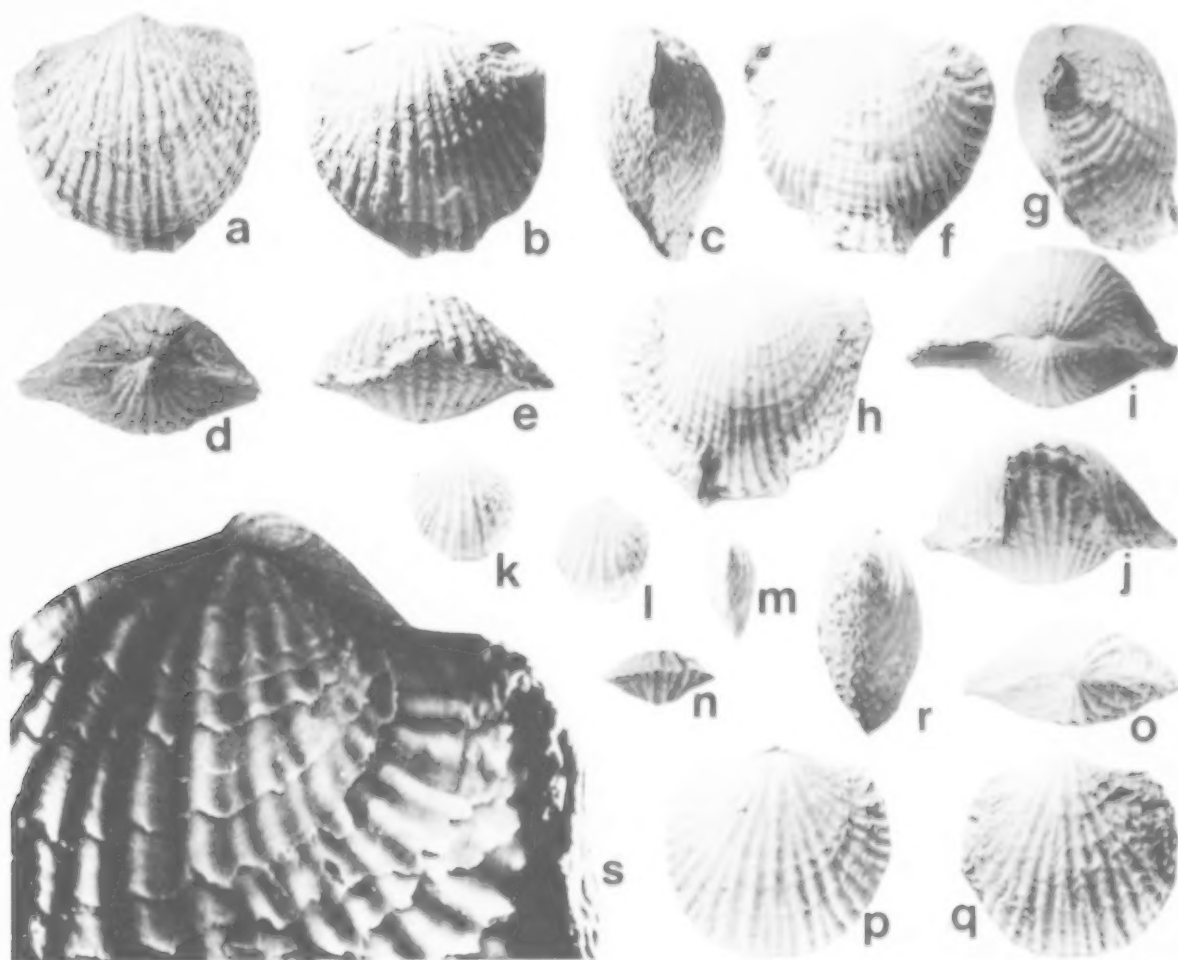


Plate 12

Figs. a–t. *Oglupes visbyensis* n. sp.

Lower–Upper Visby beds, Ygne – Rövar Lilja members, Telychian and early Wenlock.

a–e. Large specimen with prominent frill, holotype Br129636, 'Visby'.

f. Internal view of vv, Br106557, with slightly raised muscle field, type locality, Stavsklint 2, Upper Visby beds.

g–j. Paratype Br106554, type locality, Stavsklint 2.

k. Internal view of posteriorly conjoined valves, showing dv with teeth from vv sitting in sockets, Br47601, 'Visby'.

l–o. *A. cf. visbyensis*, finely ribbed form approaching rib density of *G. hedei*, paratype Br106556.

p–t. Coarser-ribbed form, paratype Br106553; all $\times 2$, except k, $\times 3$.

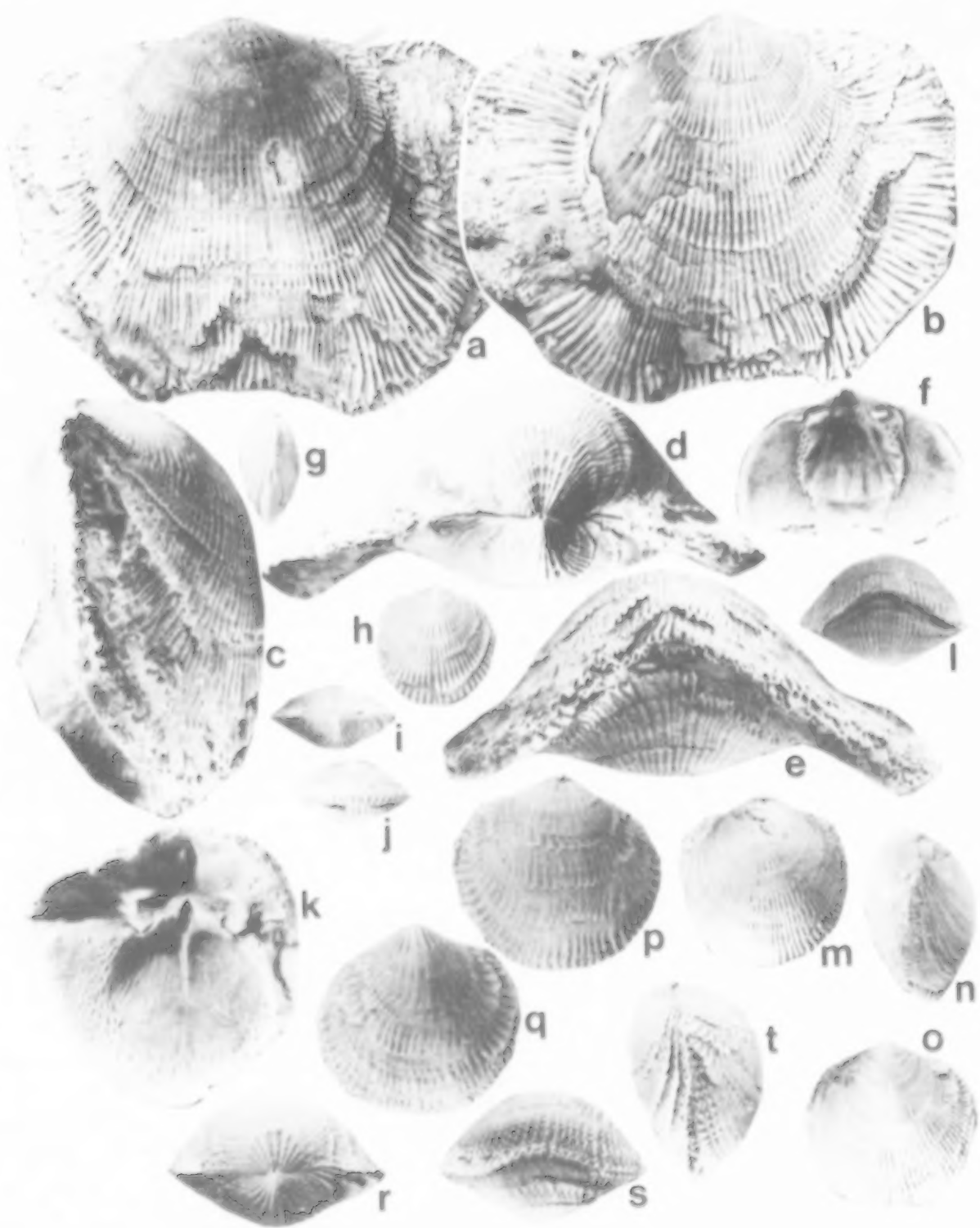


Plate 13

Figs. a–z, aa–ac. *Oglupes muldea* n. sp.

Mulde Marl, Homerian, middle Wenlock.

a–d. Holotype Br105090, Mulde Tegelbruk 1.

e–i. Smaller specimen, paratype Br105098.

j–m. Paratype smaller specimen, Br106543, Mulde Tegelbruk 2.

n–r. Paratype Br106544, Gannarve.

s–w. Neanic specimen, Br106541, Mulde Tegelbruk 2.

x, ac. Dorsal valve interior, Br106540, Mulde Tegelbruk 2, $\times 20$.

y. Dorsal valve interior, Br42476, Djupvik 1.

z. Interior ventral valve, Br106539, Mulde Tegelbruk 2.

aa. Interior ventral valve, paratype Br42478, Djupvik 1, $\times 3$.

ab. Interior ventral valve, Br42477, Djupvik 1, $\times 3$; all $\times 2$, except where marked [note great variation in muscle scars, ovarian pits].

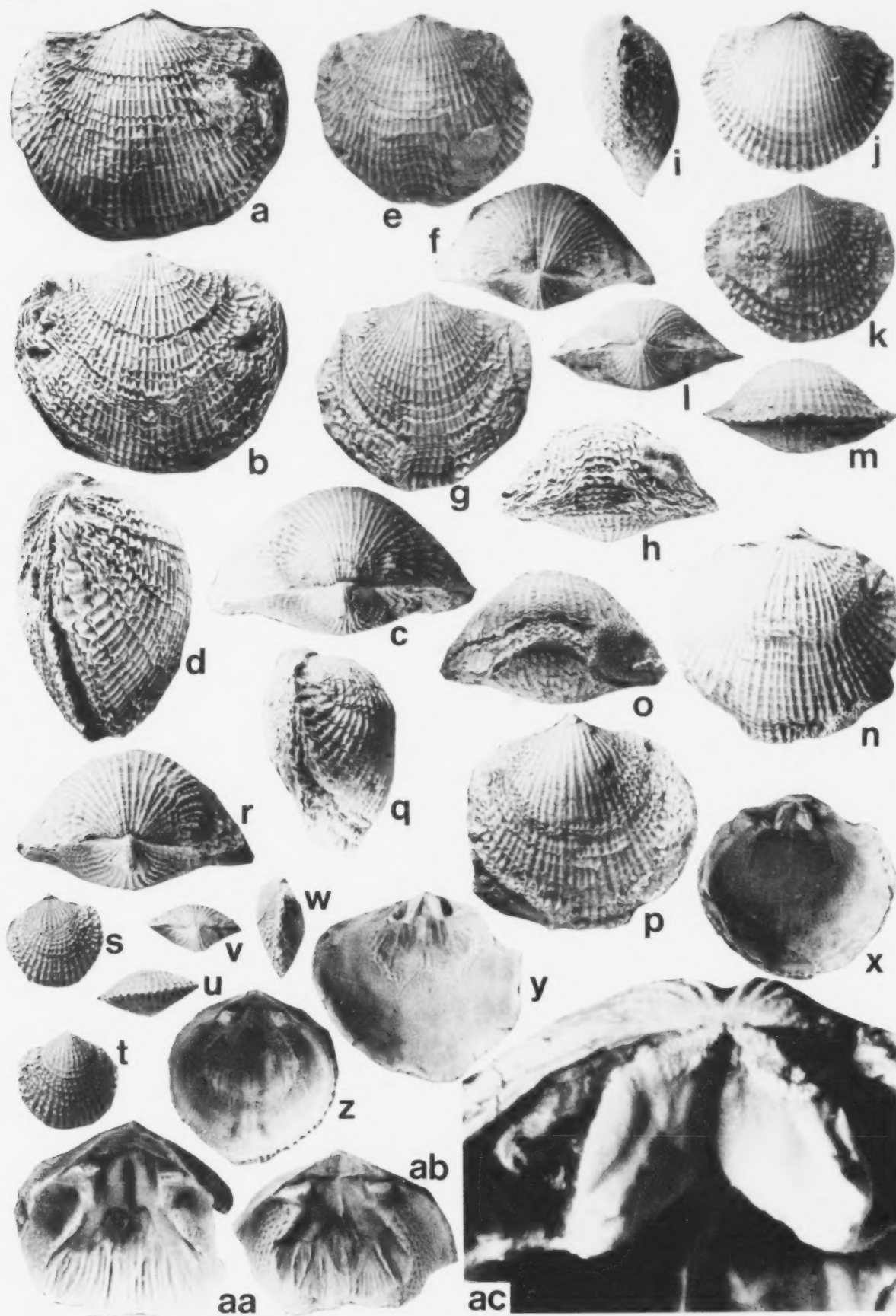


Plate 14

Figs. a–k. *Endrea echoica* Copper, 1996b

Lansa, Fårö, lower Slite beds, unit A, early Wenlock.

a–e. Paratype large shell, Br123954 [holotype illustrated Copper, 1996].

f–h. Average shell, paratype Br123955.

i–k. Smaller shell, Br123956; all $\times 2$.

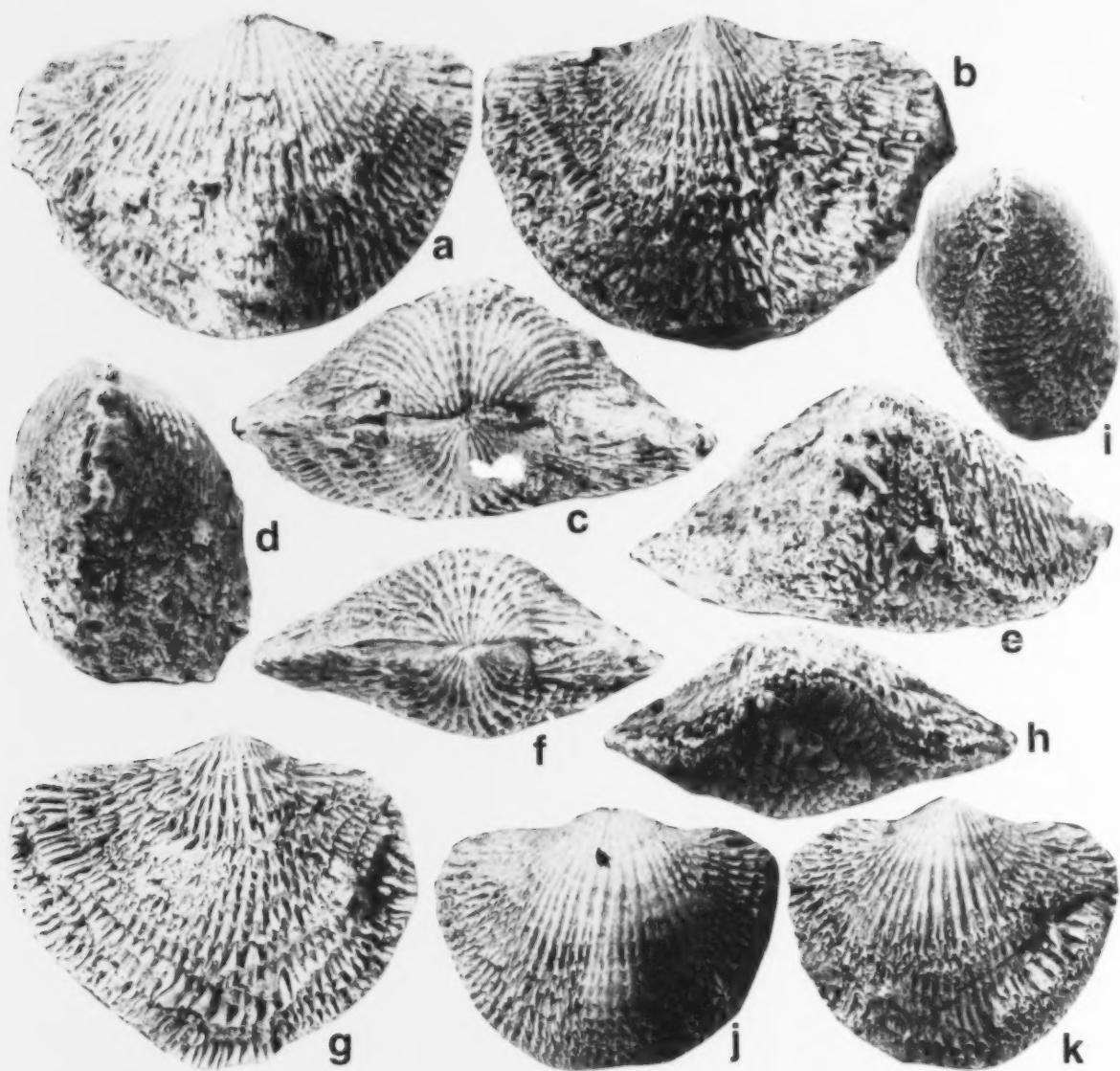


Plate 15

Fig. A, a–g. *Endrea tubulosa* (Bassett and Cocks, 1974)

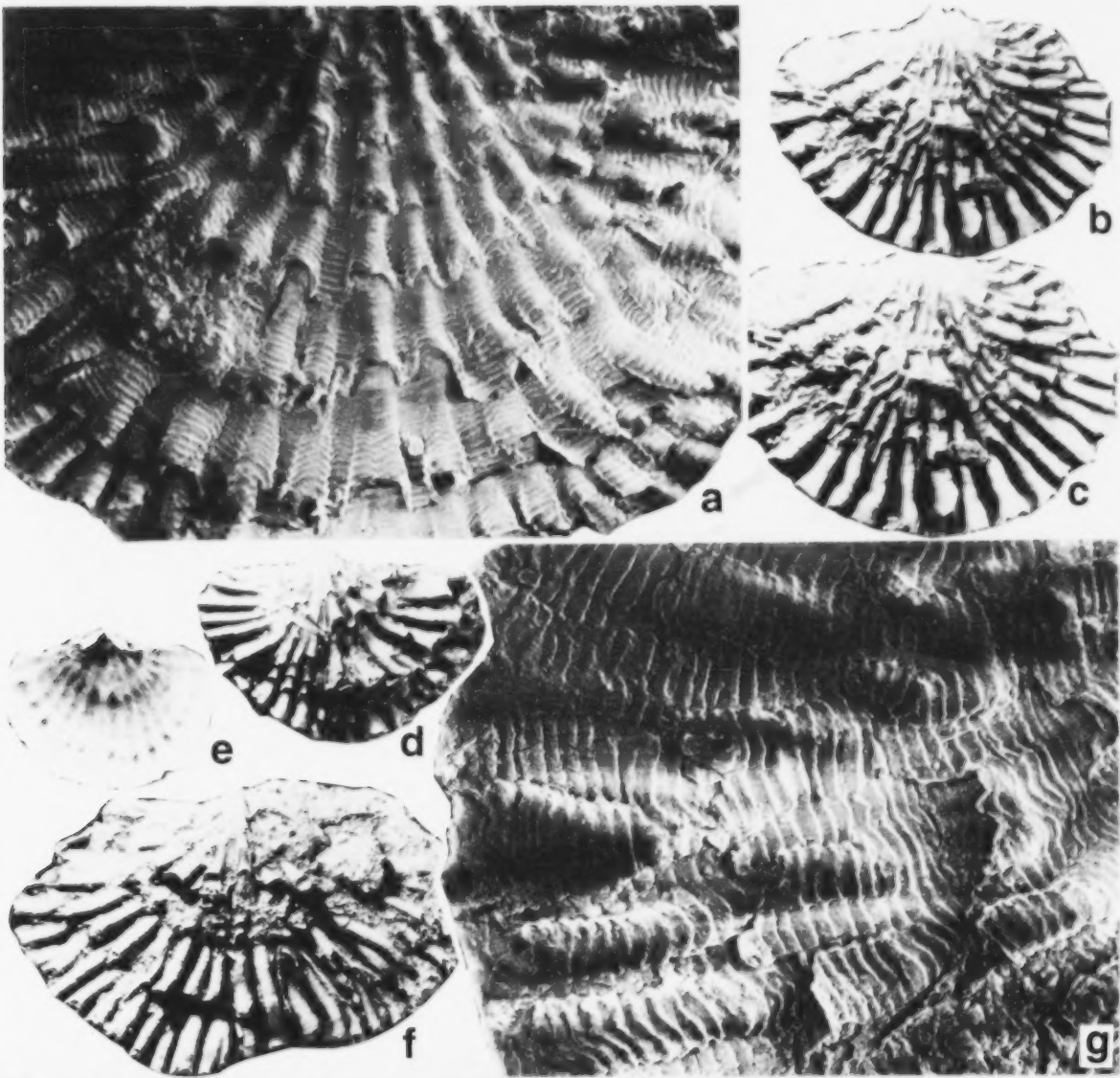
Lickershamn, Rövar Lilja Mbr., Upper Visby beds, early Wenlock.

- a. SEM photograph of hypotype Br110941, dorsal view, $\times 10.8$.
- b, c. Br43219, dorsal valve showing tubular ribs typical of species; b, $\times 3$; c, $\times 4$.
- d. Ventral view of hypotype Br43220, with typical long hinge, $\times 3$.
- e. Interior view of dorsal valve Br43221, showing thin shell, delicate hinge, $\times 3$.
- f. Ventral view of large shell, Br43219, partly obscured by sediment, $\times 3$.
- g. SEM view of Br110941, dorsal view with concentric filae, $\times 22.8$.

Fig. B. *Oglupes visbyensis* n. sp.

'Visby', Upper Visby beds, early Sheinwoodian, Wenlock. SEM close-ups of shell surface, holotype, Br129636: *left*, rib construction, $\times 11.6$; *right*, concentric growth lines, lamellae, $\times 50$.

A



B

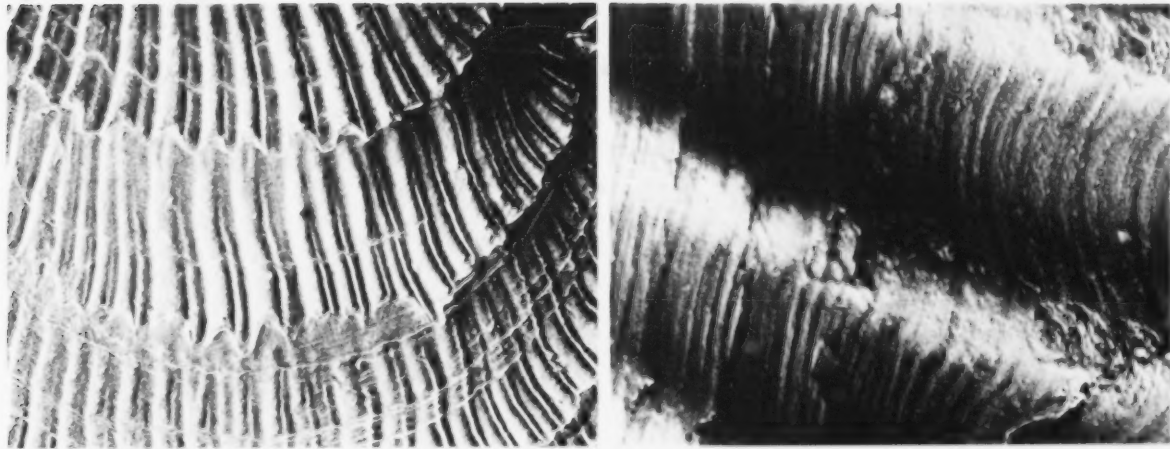


Plate 16

Fig. A, a–t. *Endrea lonsdalei* (Alexander, 1949)

'Dudley Castle Hill', Dudley Limestone, late Wenlock (Alexander colln.).

a–e. Holotype A11622 (selected by Alexander, 1949), with loss of frills on one side of hinge.

f–j. Paratype A30424, specimen with less sharply defined fold.

k–o. Immature shell A30422, showing expansion of rib size.

p–t. Small specimen A30423; all $\times 2$.

Fig. B, a–n. *Endrea ekenia* n. sp.

Laubackar 1, Eke Formation, middle Ludlow.

a–d. Adult shell, holotype Br106592.

e–i. Medium-sized paratype Br106593.

j–n. Neanic paratype Br106594, $\times 2$.

Fig. C, k–n. *Plectatrypa* (*Plectatrypa*) *parimbricata* n. sp.

'Lerberget', Stora Karlsö, Slite beds, middle Wenlock.

k–n. Large specimen, holotype Br108058, $\times 2$.

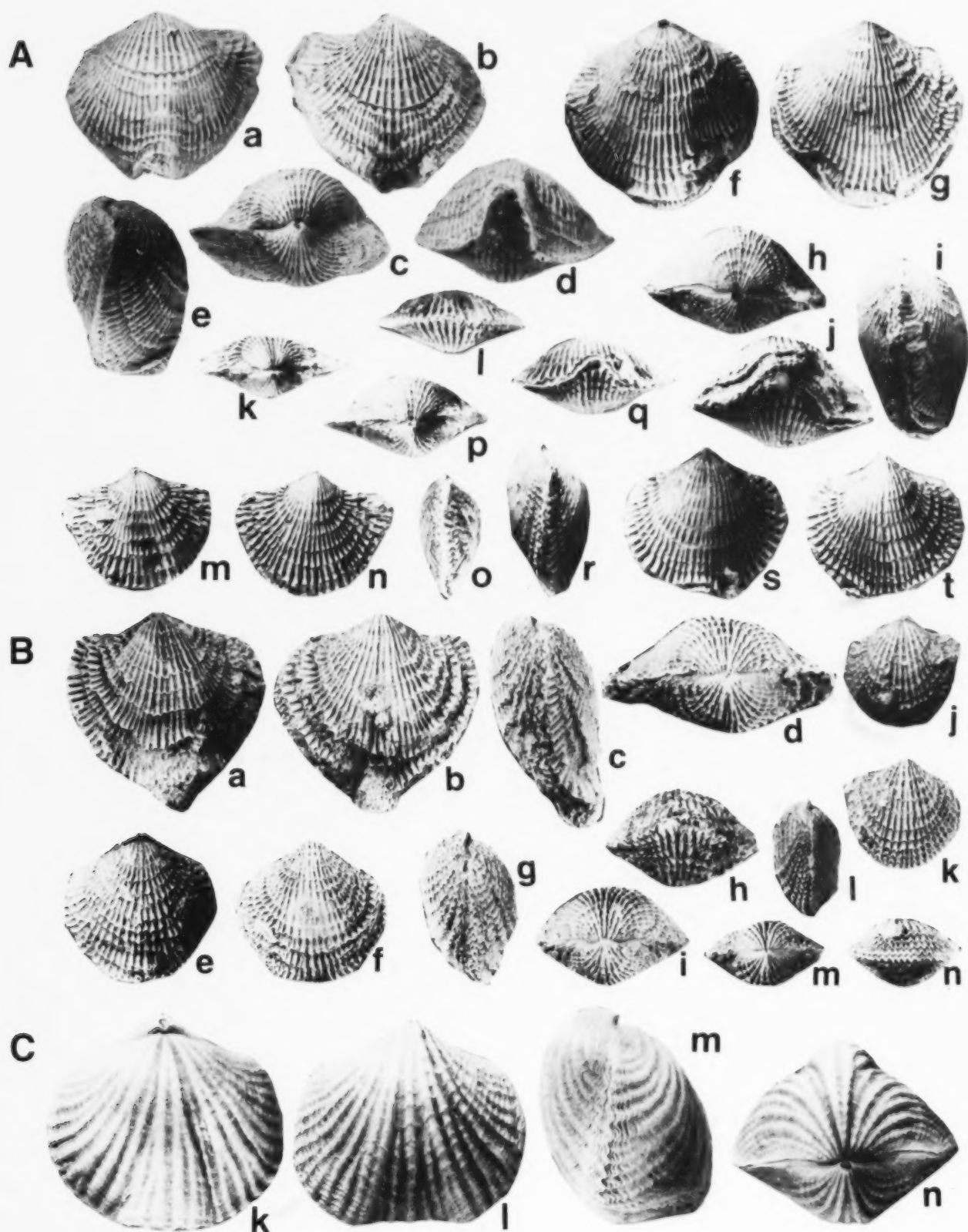


Plate 17

Fig. A, a–n. *Reticulatrypa hamrae* n. sp.

'Hoburgen', Hamra Fm., Ludfordian, late Ludlow.

a–f. Holotype Br10870, well-preserved specimen; a–d, $\times 2$; e, SEM photo of ribs and growth lamellae extended into 'pseudospines', $\times 48.7$; f, SEM photo of concentric filose ornament, $\times 64.7$.

g–j. Paratype Br42694, smaller specimen, $\times 2$, except j, $\times 8$.

k. Internal view of umbonally damaged ventral valve, paratype Br105864, $\times 2$.

l–n. Neanic specimen, paratype Br42697, showing early growth stages with narrower apical angle, proportionally prominent beak and area.

Fig. B, a–t. *Atrypina* (*Atrypina*) *buildwasensis* n. sp.

'Buildwas', Shropshire, Buildwas beds, *centrifugus*–*murchisoni* zones, early Wenlock.

a–e. Neanic specimen, paratype BB55143.

f–j. Average specimen with encrusting bryozoan on dorsal valve, paratype BB55147.

k–o. Holotype BB55146.

p–t. Paratype BB55154, specimen with fewer growth lamellae, stronger mid-rib pair; all $\times 2$.

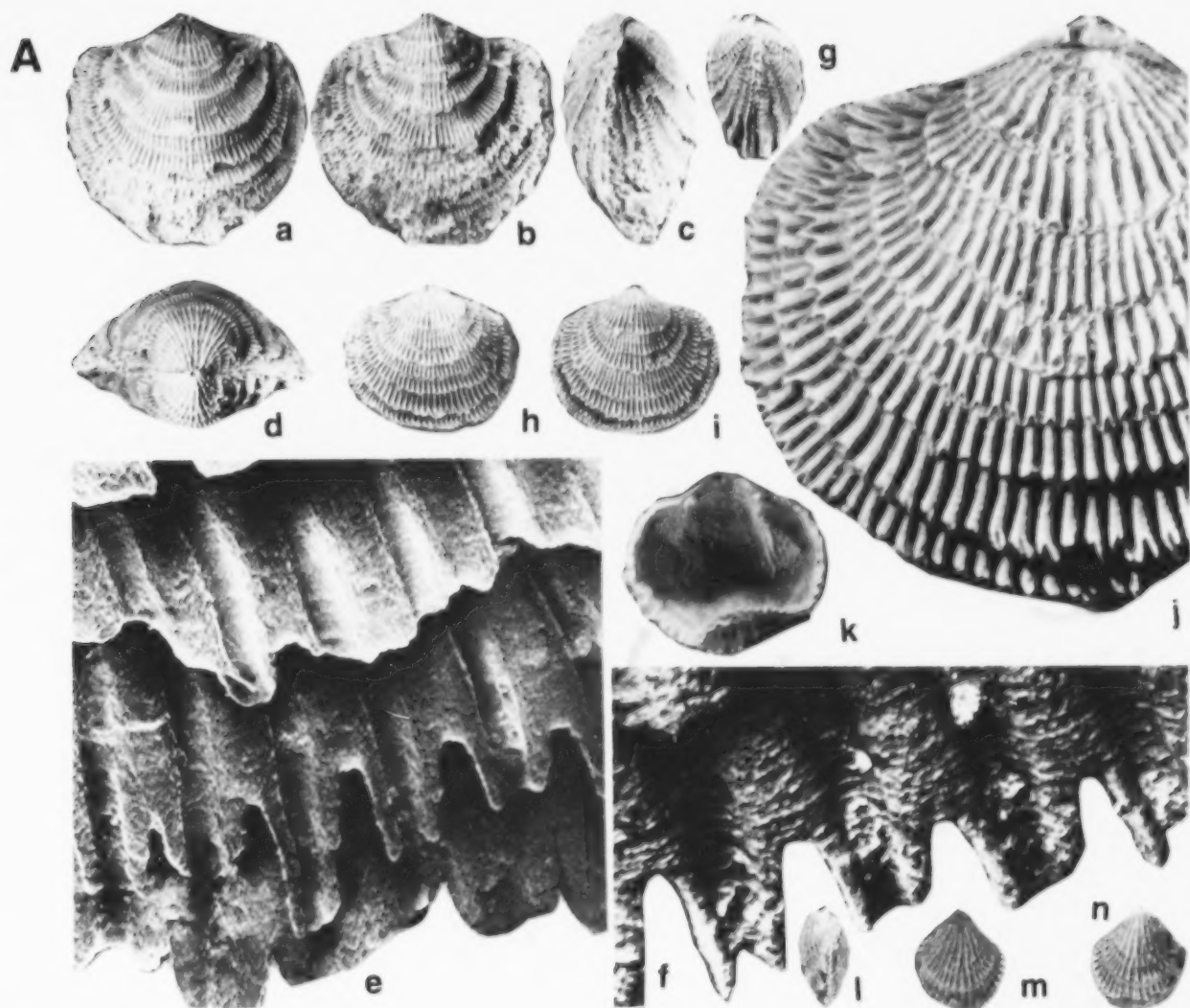


Plate 18

Fig. A, a–m. *Atrypina (Atrypina) barrandii* (Davidson, 1848)

Wenlock Shale '[high]', Walsall, and upper Slite beds, Klinteberg beds, middle–late Wenlock.

a–e. Hypotype Br50051, 'Utholmen, Vastergarn sn.', upper Slite beds, $\times 3$.

f–j. Hypotype Br50052, 'Utholmen', $\times 3$.

k. SEM photograph of hypotype Br134683, $\times 20.8$.

k–m. SEM photos of dorsal and ventral valve, Br134682, $\times 24$

[k–m. SEM photos of specimens from Hunninge 1, Klinteberg beds.]

Fig. B, a–m. *Atrypina cf. gallina* (Haupt, 1878)

Hamra beds, Whitcliffian, late Ludlow.

a–e. Typical specimens, Br134661, all $\times 4$, except ventral view 'e', $\times 2$.

f. Dorsal valve interior, Br134662, $\times 3$.

g. Br134663, ventral valve interior, $\times 3$ (from Kättelviken 1).

h, i. Reproduction of figs. 16c–d, *Atrypina gallina* (Haupt, 1878), showing close similarity with Gotland specimens (scale approx. $\times 2$).

j–m. Small specimen, Br121546, Burgsvik, $\times 4$.

Fig. C, a–r. *Plectatrypa (Plectatrypa) imbricata* (Sowerby, 1839)

Farley Mbr., Coalbrookdale Fm. to Much Wenlock Limestone, late Wenlock.

a–e. Neotype BB55347, 'Wenlock Shale, Tame Bridge, Walsall'.

f–i. BB27099, paraneotype from the 'Wenlock Limestone, Dudley'.

j–n. Paraneotype BB8610, smaller specimen, 'Wenlock Limestone, Dudley'.

o–r. Neanic specimen, paraneotype BB97775, 'Wenlock Limestone, Dudley'.

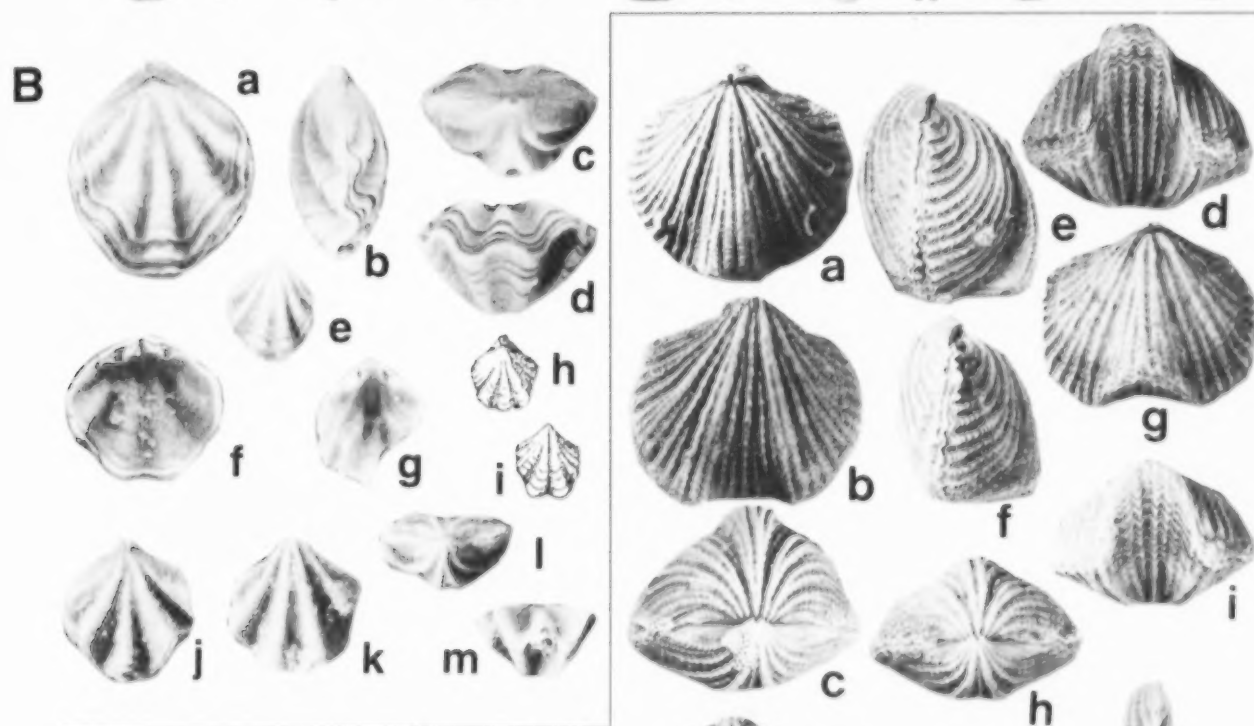
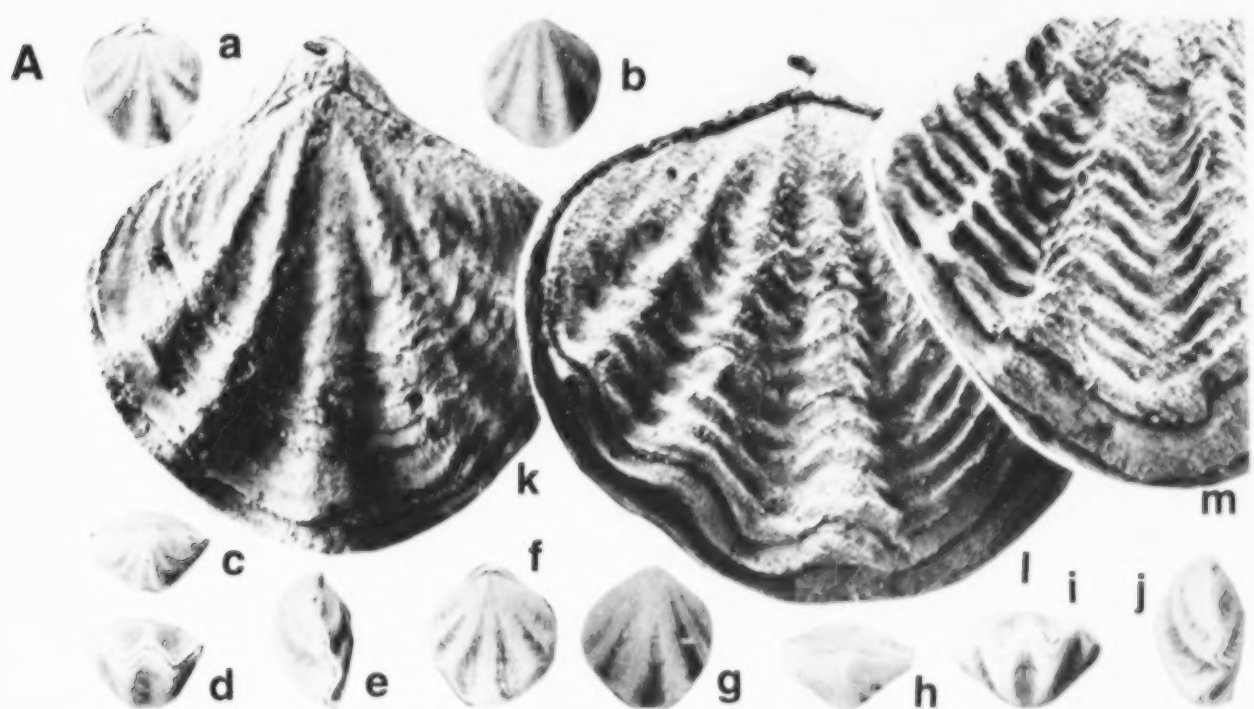


Plate 19

Fig. A, a–z, aa. *Plectatrypa (Plectatrypa) abbreviata* (Sowerby, 1839)

Wenlock Shale, Buildwas beds, *centrifugus*–*murchisoni* zones, early Wenlock.

a–g. Holotype by monotypy GS6600, 'Wenlock Shale, Woolhope' [c, d, copies of the Sowerby, 1839, pl. 13, fig. 27, expanded to $\times 2$].

h–l. Hypotype BB27879, a larger specimen with bryozoan epibiont on fold, 'Buildwas', Buildwas Fm.

m–q. Hypotype BB3244a, Wenlock Shale, Malverns.

r–v. Br55283, identical to Buildwas specimens, Häftingsklint, Högklint beds, early Wenlock.

w–z, aa. Br47352, Kopparsvik, Upper Visby beds, early Wenlock.

Fig. B, a–j, o–s. *Plectatrypa (Plectatrypa) parimbricata* n. sp.

Slite beds, middle Wenlock.

a–e. Paratype Br110940, Västergarn.

f–j. Wider specimen, paratype Br110939, Västergarn.

o. Large specimen, Br108058, holotype, Lerberget, Stora Karlsö.

p–s. Paratype Br108044, immature specimen, Västergarnshamn; all $\times 2$.

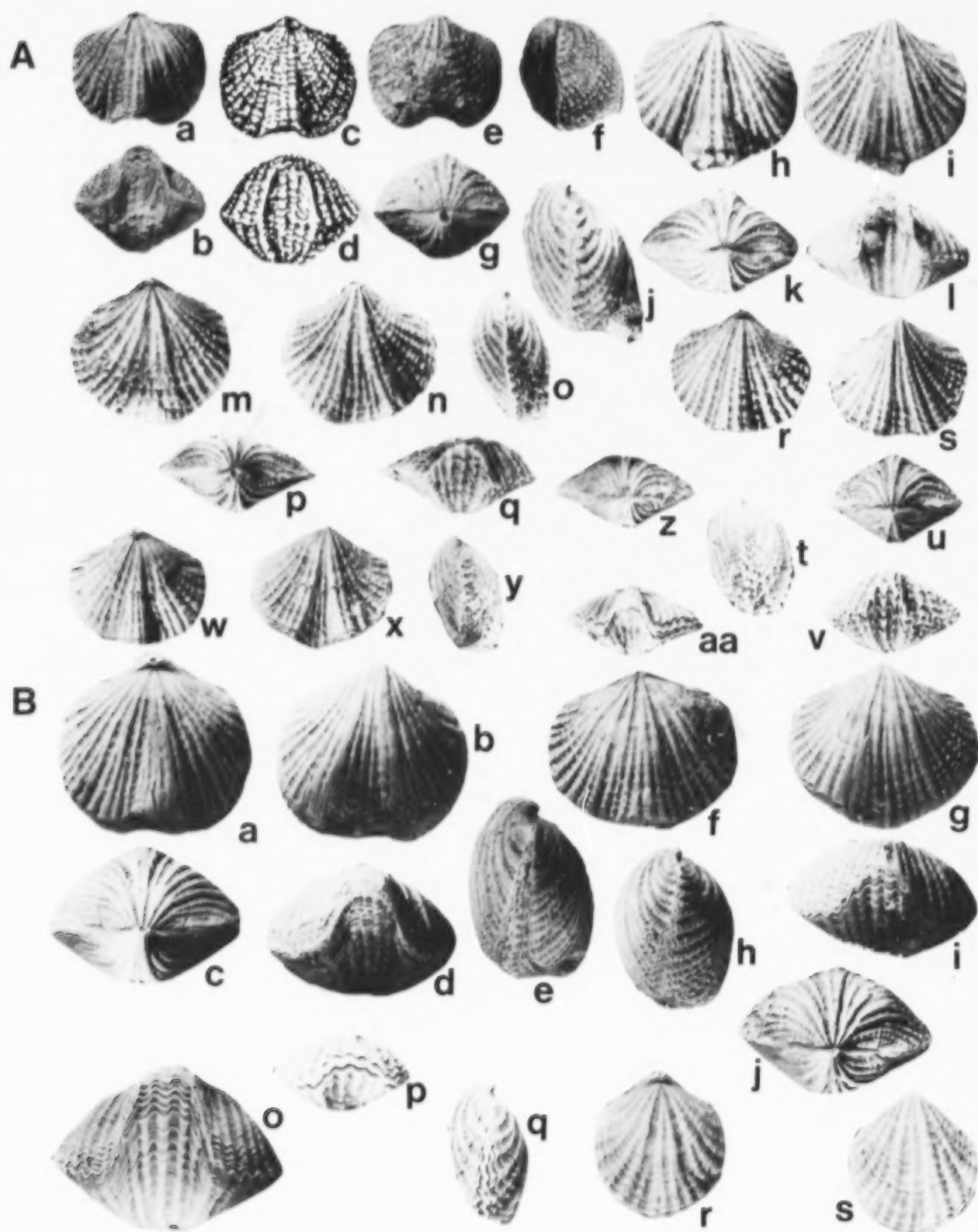


Plate 20

Fig. A, a–m. *Plectatrypa* (*Gutnia*) *capidula* Copper, 1996b

Tjälderholm 1, upper Slite beds.

a–g. Holotype medium-sized specimen Br46461, a–e, $\times 3$.

f–m. Gerontic shell, showing evenly sized ribs, Br41635, $\times 2$.

Fig. B, n–s. *Xanthea lamellosa* (Lindström, 1861)

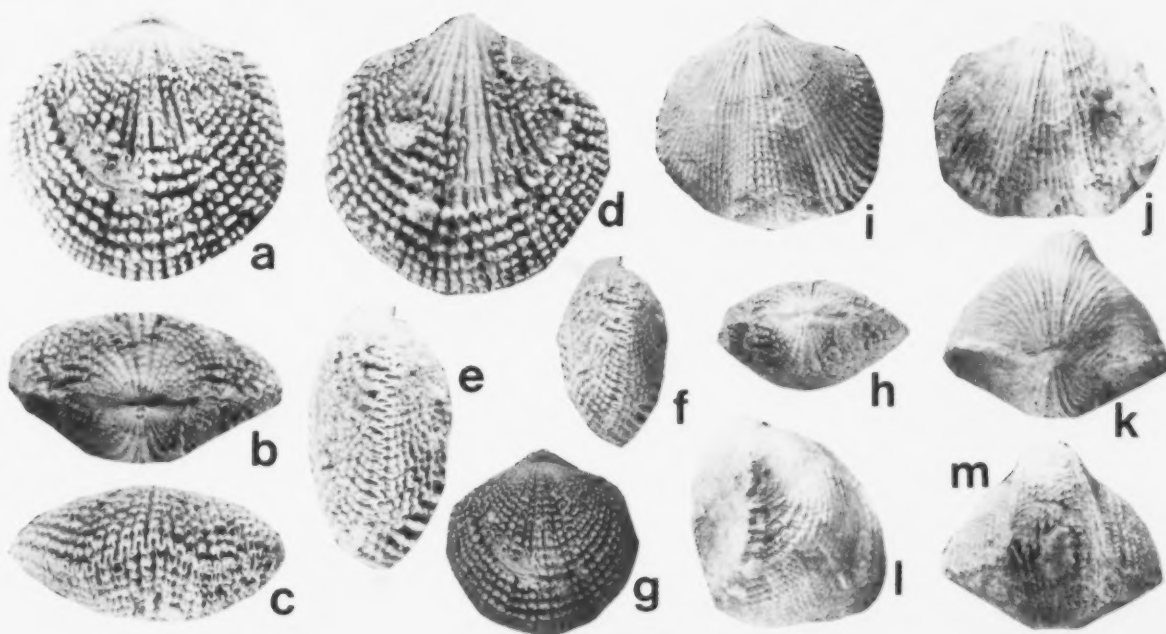
Balsklint, Högklint beds, early Sheinwoodian, early Wenlock; paratype Br103389.

n. Detail of dorsal valve, $\times 4$.

o–r. Views of shell at $\times 2$.

s. SEM close-up of shell surface on dorsal valve $\times 99.2$.

A



B

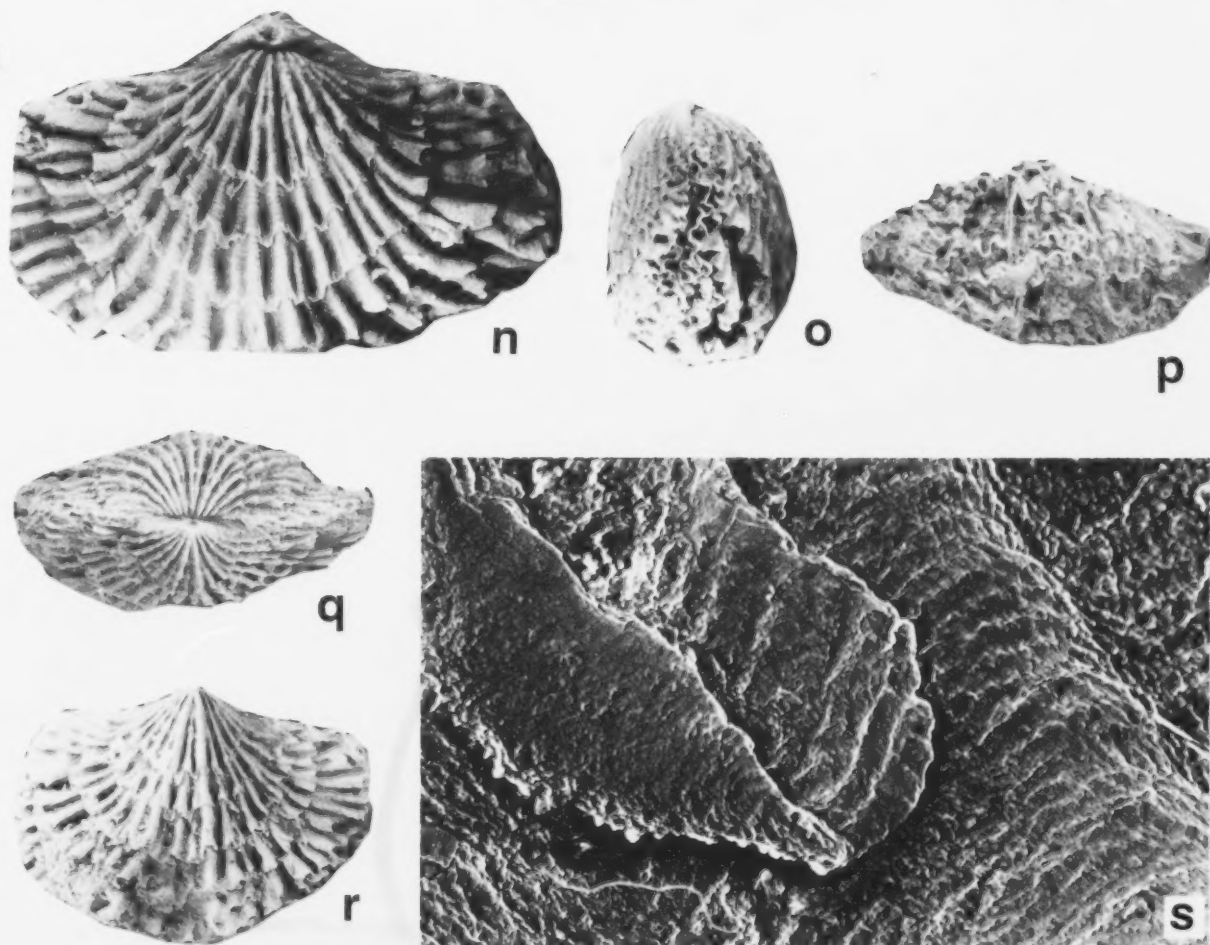


Plate 21

Fig. A, a–u. *Xanthea scabiosa* n. sp.

'Snäckgärdet, Visby', Upper Visby beds, early Sheinwoodian.

a–e. Holotype Br107478, large specimen with narrow, high fold, single rib in ventral sulcus.

f–j. Small specimen, Br107475, showing some comparisons with 'spinatrypid' ornamentation.

k–o. Medium-sized specimen, Br107476, with 2 ribs on ventral sulcus.

p–s. Larger specimen Br107477, with single rib in ventral sulcus.

t. SEM photograph of shell surface, $\times 25.6$.

u. SEM close-up of micro-ornament showing zigzag microfilae, $\times 104$.

Fig. B, a, b. *Xanthea scabiosa* n. sp.

Upper Visby beds, 'Snäckgärdet, Visby', early Sheinwoodian.

a. SEM photograph of the micro-ornament on the ribs, $\times 29.6$.

b. SEM close-up of the secondary layer with overlying primary layer on left side, and overlapped underlying primary layer on lower right, with zigzag micro-ornament as seen in *Xanthea* (enlargement of lower right rib crest on Fig. A, a), $\times 210$.

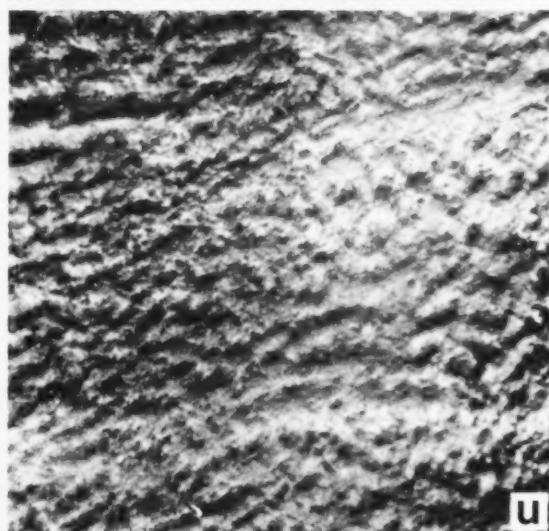
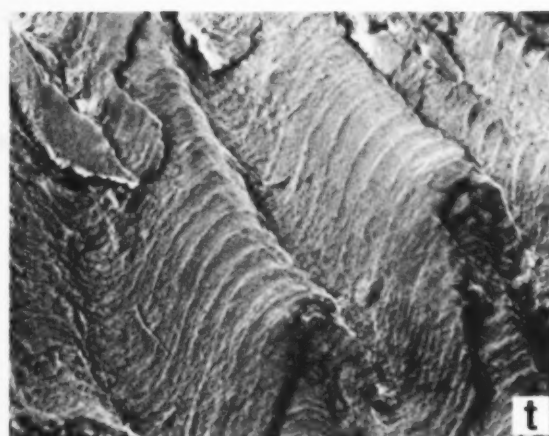
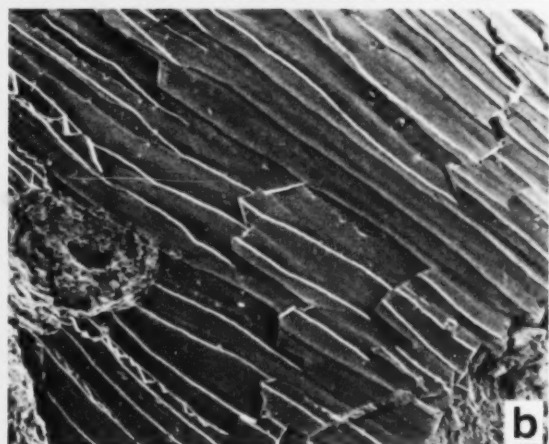
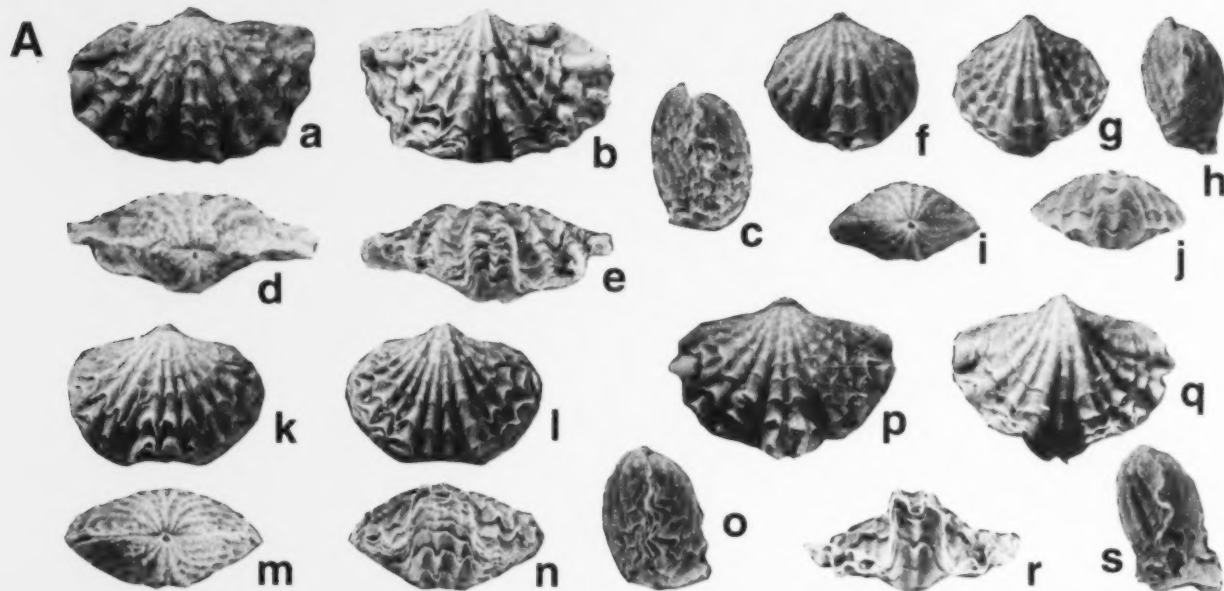


Plate 22

Fig. A, a–x. *Xanthea haruspex* n. sp.

Slite beds, middle Wenlock, Gotland; and Much Wenlock Limestone, U.K.

a–e. Holotype Br105878, with broken ventral umbo, Fjaugen.

f–j. Small specimen, Br103441.

k. Internal view of ventral valve, Br105881, Fjaugen.

l–n. Paratype Br103877.

o–s. Medium shell, paratype BMB20701, 'Dudley'.

t–x. Paratype Birmingham Colln. #643, Dudley, probably Lower Quarried Limestone; note resemblance to *Eospinatrypa*; all $\times 2$.

Fig. B, c–l. *Eospinatrypa asperula* (Davidson, 1882), late Wenlock, Homerian, U.K.

c–l. Hypotype BB66829, 'old Wenlock Limestone quarries at Benthall Edge', late Wenlock.

c–g. Views of whole shell, $\times 2$.

h–l. Hypotype A26589, 'Dudley, Dudley Limestone', with capidulae or spine bases on central left side of vv, $\times 2$.

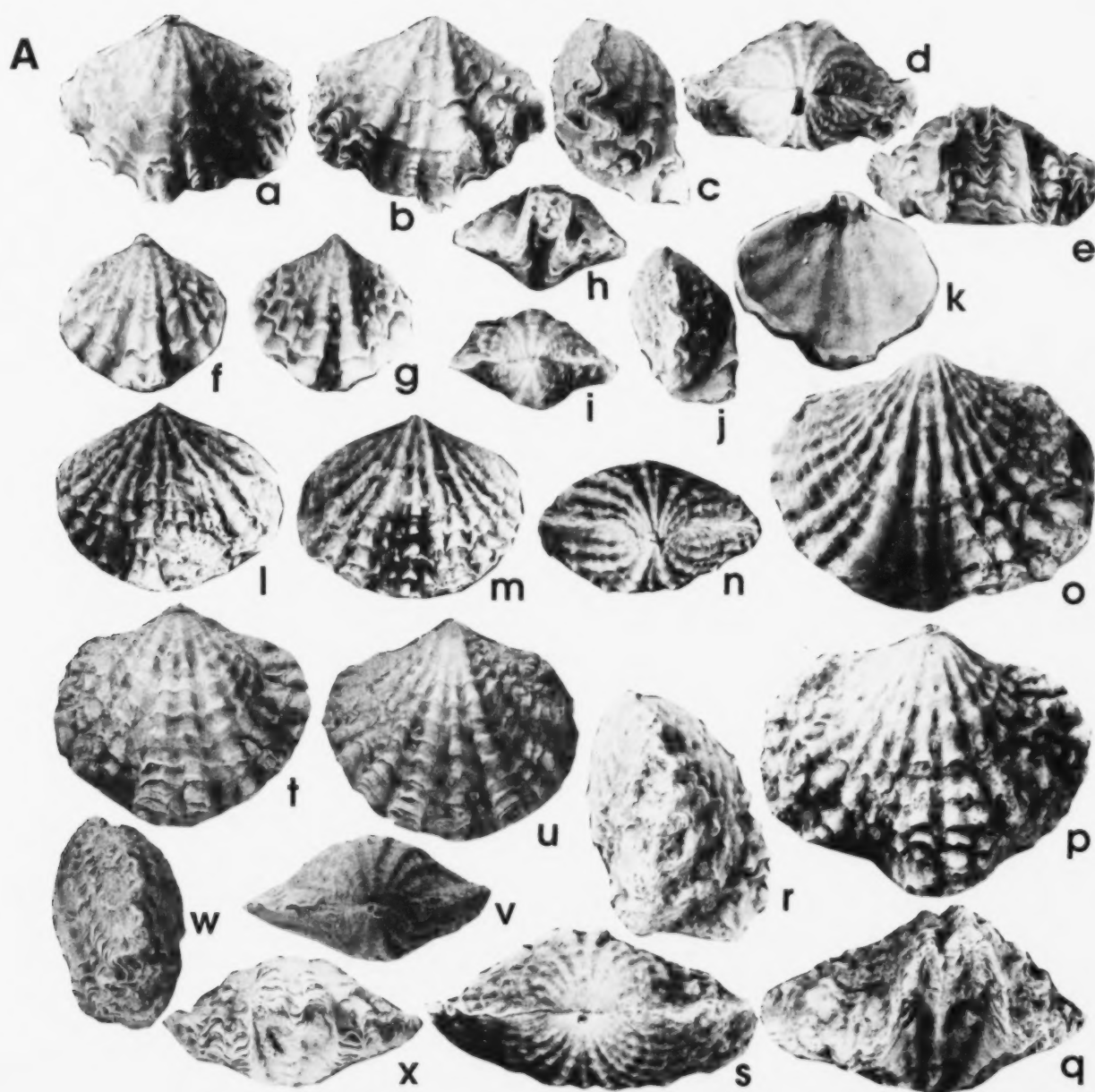


Plate 23

Fig. A, a–o. *Eospinatrypa hallae* n. sp.

Halla Formation, middle–late Wenlock, Homerian.

a–e. Paratype immature specimen Br105917, 'Hörsne Kyrkan, kanal vid kyrkan'.

f–j. Immature shell, paratype Br105928, 'Hörsne kanalen'.

k–o. Globose, mature specimen, holotype Br105911, all $\times 2$.

Fig. B, a–z, za. *Spirigerina marginalis* (Dalman, 1828)

'Klinteberg', late Wenlock.

a–e. Paratype Br123223, well-preserved specimen with high fold.

f–j. Paratype Br123225.

k–o. Lectotype Br105813, slightly worn specimen from Hisinger type collection, most closely approaching original Dalman illustration.

p–t. Relatively wide specimen, paratype Br123224.

u–y. Immature specimen, paratype Br105809.

z. Interior of dorsal valve Br41937.

za. Interior of ventral valve, paratype Br30833, showing foramen, flanking thick deltidial plates; all $\times 2$.

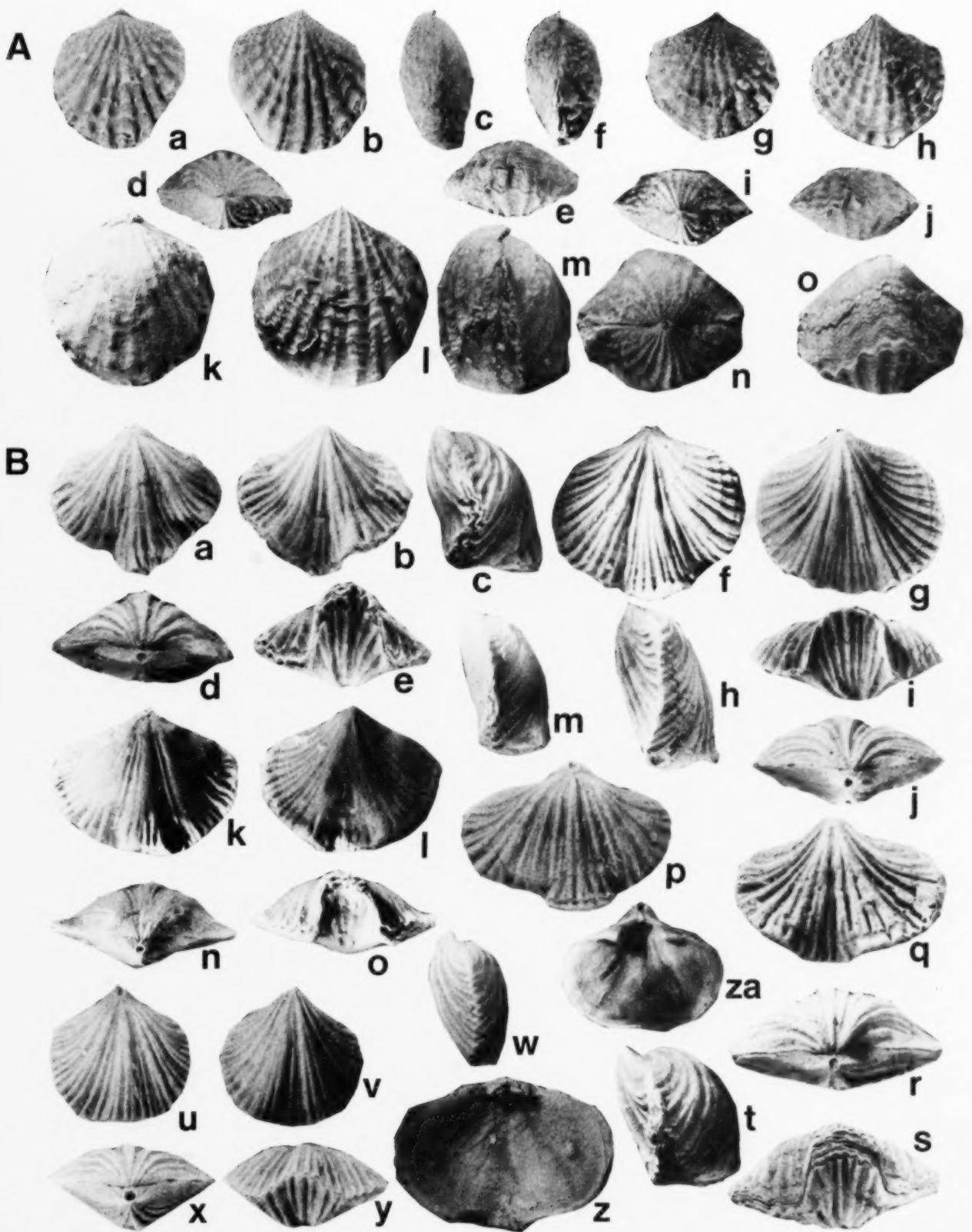


Plate 24

Figs. a–z, ta–tn. *Spirigerina lockwenia* n. sp.

Much Wenlock Limestone, late Wenlock, *ludensis* Zone, Wenlock Edge area.

- a–e.** Paratype GS6601, one of six specimens from the Sowerby collection in the Geological Survey Museum, identical to the Sowerby illustration (1839, pl. 12, fig. 12, right hand), labeled 'Wenlock Limestone, Wenlock Edge' [N.B. BB108 is also similar to the Sowerby type, but is here suggested not to be the figured specimen].
- f–j.** Well-preserved specimen with short frill, encrusting bryozoan on ventral valve, holotype BB2143, 'old quarry Bower's Brook'.
- k–o.** Paratype BB9868a.
- p–r.** Paratype BB34777, large specimen with wide area.
- s–u.** Hypotype BB2146, Much Wenlock Limestone, 'Bower's Brook, old quarry'.
- v–x.** Hypotype BB83198, Wenlock Limestone, Lincoln Hill.
- y, z, ta–tc.** Hypotype BB55168, Wenlock Limestone, Tickwood.
- td–th.** Hypotype BB55167, Much Wenlock Limestone, Tickwood.
 - ti.** Small slab, BB55169, Much Wenlock Limestone, Tickwood; all $\times 2$.
- tj–tn.** Sowerby collection, GS12169, Wenlock Edge.

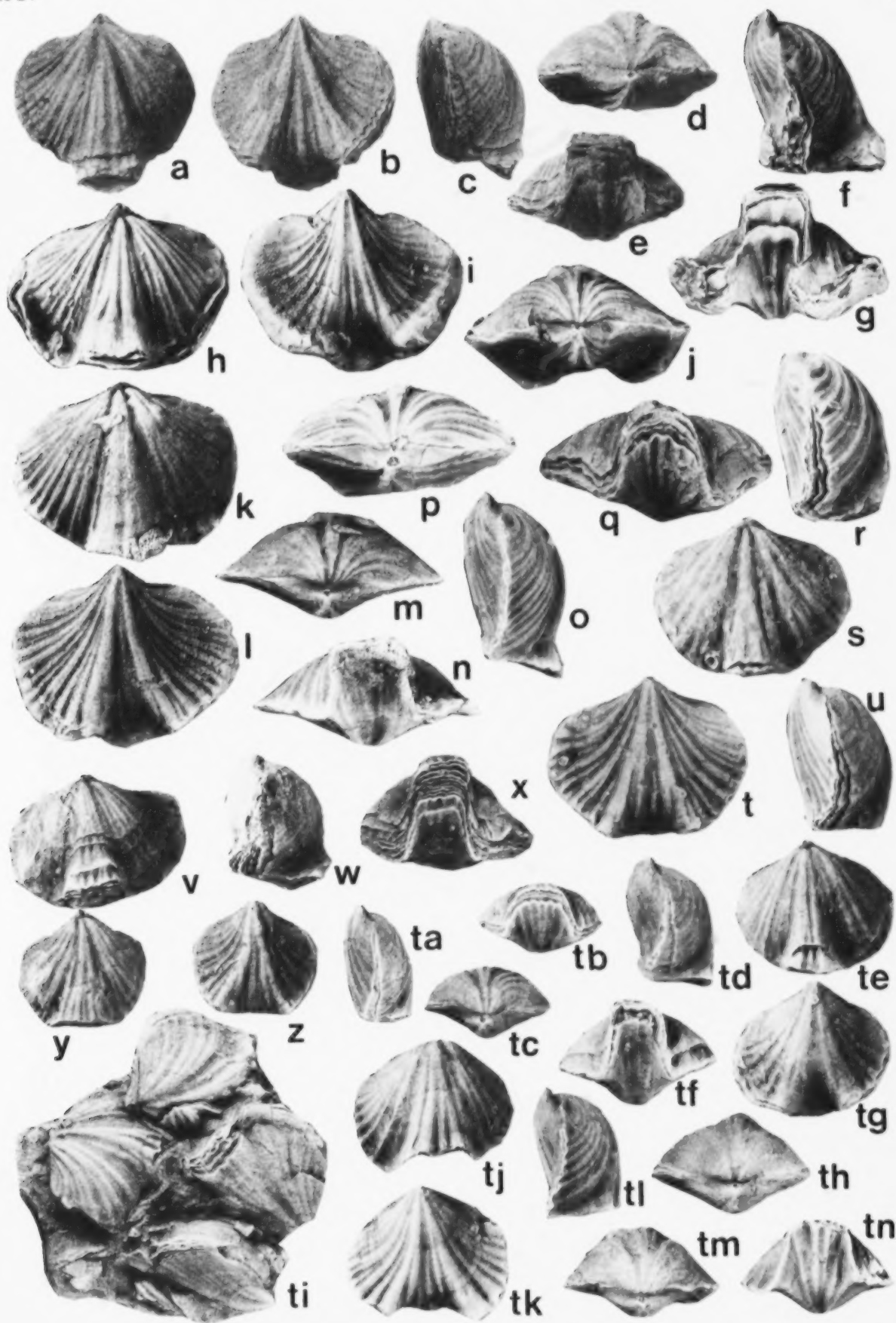


Plate 25

Fig. A, a–o. *Spirigerina costata* (Lindström, 1861)

Hemse beds, units C–E, early Ludlow, all from type locality Sandarve Kulle.

a–e. Lectotype Lindström collection, typical wide shell, Br42072.

f–j. Immature shell with up to 10 ribs on the dv, Br107509.

k–o. Wide, coarsely ribbed shell, Br42073; all $\times 2$.

Fig. B, a–r. *Spirigerina quinquecostata* (Munthe, 1911)

Hoburgen 2, Hamra beds, late Ludfordian, Ludlow.

a–e. Average specimen, neotype Br106550, with 5 strong ribs on the dv, 6 on the vv.

f–j. Large, partially crushed specimen, paraneotype Br106551.

k–o. Average specimen with 5 ribs on dv and intercalated 5 smaller ribs, mid-rib bifurcating.

p. Internal view of dorsal valve, paraneotype Br106552; $\times 2$.

q. SEM photo of surface micro-ornament, $\times 83.8$.

r. SEM close-up of micro-ornament showing very fine radial ridges and concentric filae, $\times 139$ [both SEM of Br106551].

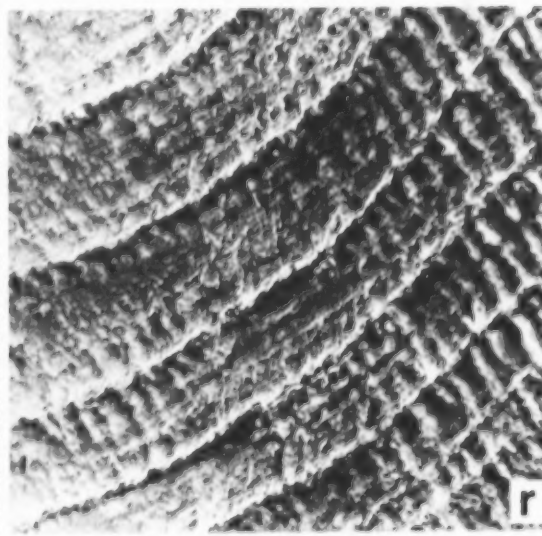
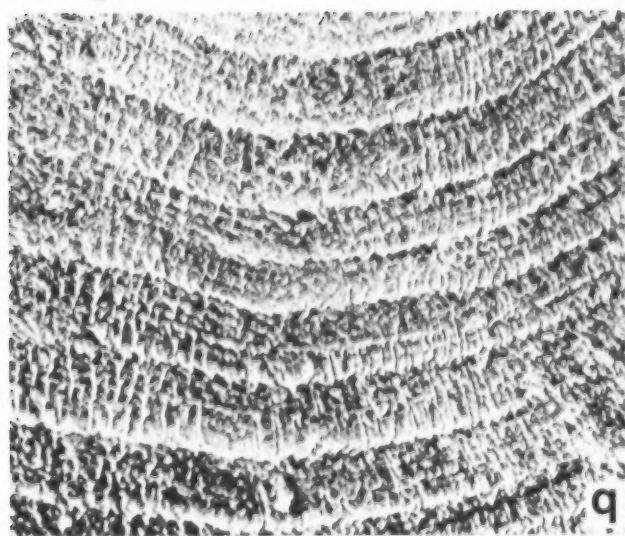
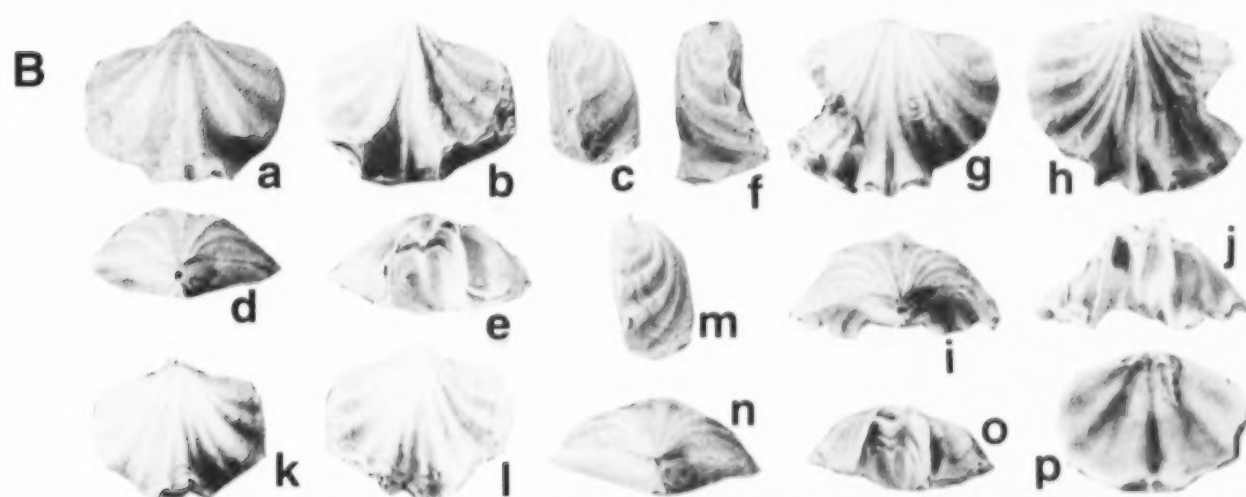


Plate 26

Fig. A, a–l. *Lissatrypa* cf. *minuta* (Rybnikova, 1967)

Harley Brook, Hughley Shale, Telychian.

a–d. Small, smooth shell, hypotype BC11274a [BMNH].

e–h. Specimen with concentric surface fibres, hypotype BC11274b.

i–l. Hypotype BC11274c; all $\times 2$.

Fig. B, a–m. *Lissatrypa obovata* (Sowerby, 1839)

Dudley and Mathon Lodge, Britain, 'Ludlow Shale' and Much Wenlock Limestone.

a–e. Lectotype GSM6624, a Sowerby specimen with a moderate anterior fold, 'Mathon Lodge', ?early Ludlow, $\times 2$.

f–j. Hypotype BB5497, typical specimen from the 'Much Wenlock Limestone', Dudley, late Wenlock, $\times 3$.

k. Ventral valve, with pedicle collar, diductors lacking dividing septum, hypotype B619a, Dudley, $\times 3$.

l. Hypotype B619b, ventral valve, B619b, with septum dividing diductors, Dudley, $\times 3$.

m. Hypotype A26477, with typical *Lissatrypa* hinge plate structure, lacking cardinal pit, Dudley, $\times 3$.

Fig. C, a–e. *Lissatrypa compressa* (Sowerby, 1839)

Holotype by monotypy from Murchison collection, GS6625, labeled '*Rhynchonella compressa*, Woodside, Wenlock Shale', identifiable as the specimen illustrated by Sowerby 1839. The precise horizon is unknown; early Wenlock, $\times 2$.

Fig. D, a–j. *Septatrypa karlsoa* n. sp.

Stora Karlsö, upper part of Slite beds, middle Wenlock.

a–e. Holotype Br124739, large, mature specimen from 'Lerberget' [probably = Lerberget 4].

f–j. Paratype Br106529, immature shell, Ramroir 1; all $\times 2$.

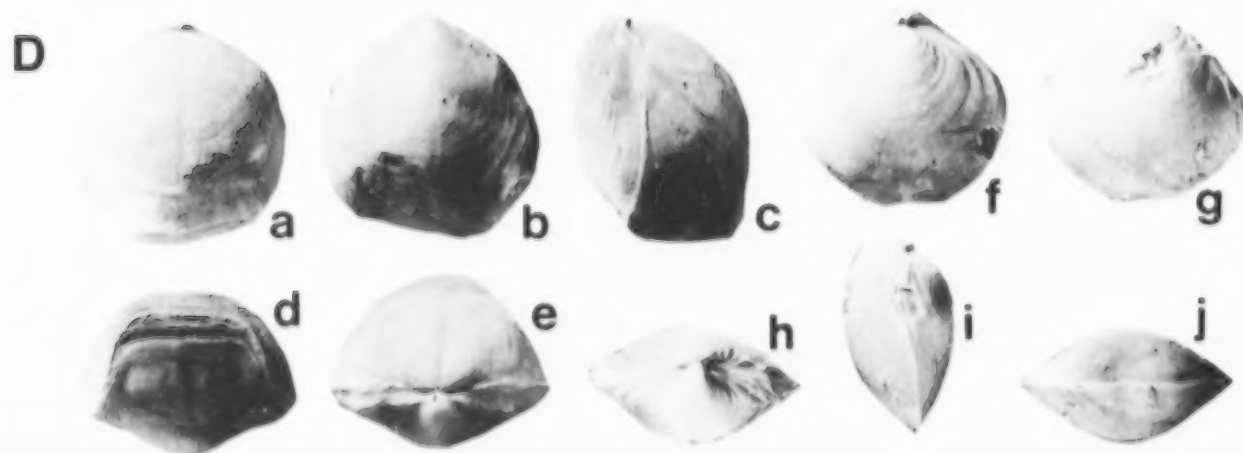
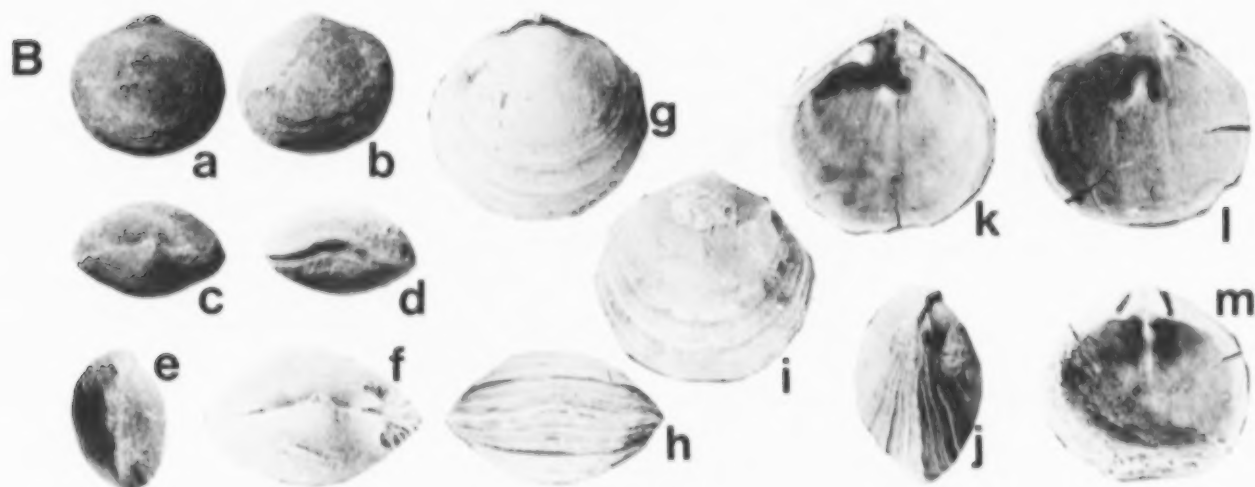


Plate 27

Fig. A, a–q. *Atrypoidea sulcata* (Lindström, 1861)

Unit A, lower Hemse Fm., early Ludlow, NE coast, Garnudden 1 (= ca. 'Hammarudd').

a–e. Paratype from Lindström collection, Br44650, 'Hammarudd' — note the thin narrow groove in the plane of symmetry on each valve, which gave rise to the name of the species.

f–j. Paratype Br44600, gerontic specimen, Lindström collection, 'Hammarudd'.

k. Hypotype Br106569, showing a decorticated shell with faint, parallel vascular canals, Garnudden 5.

l. Hypotype Br106568, decorticated ventral valve showing internal mould with parallel vascular canals.

m–q. Hypotype smaller neanic specimen, hypotype Br106566, Garnudden 5; all $\times 2$.

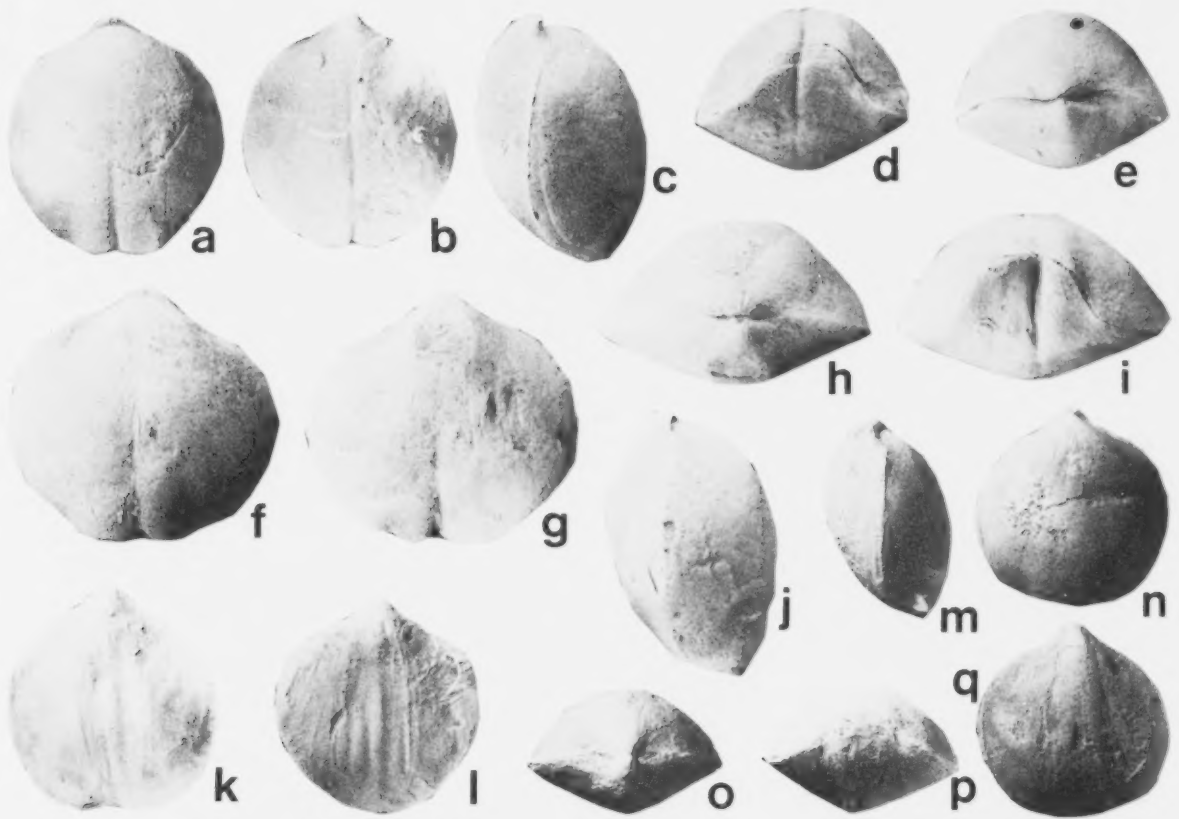
Fig. B, a–j. *Atrypoidea hemsea* n. sp.

Tänglings Hallar, upper Hemse Formation, unit E, middle Ludlow.

a–e. Paratype Br108469, immature shell.

f–j. Holotype Br108468, typical larger shell; $\times 2$.

A



B

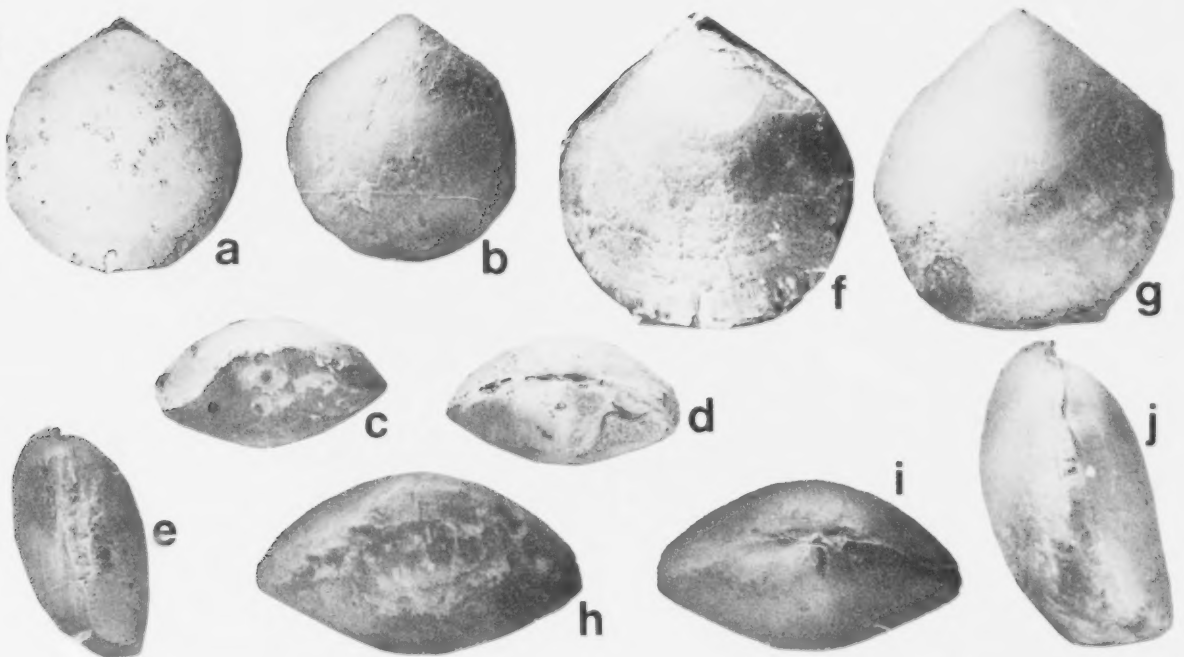


Plate 28

Figs. a–r. *Atrypoides prunum* (Dalman, 1828)

Ganne 1, Hemse beds, units C–D, early Ludlow.

a–d. Immature shell, hypotype Br106558, with gentle anterior fold.

e–h. Medium-sized shell, hypotype Br106560.

i–m. Gerontic specimen, Br106563, with narrow outline, highly globose profile.

n–r. Wide gerontic shell, hypotype Br106562.

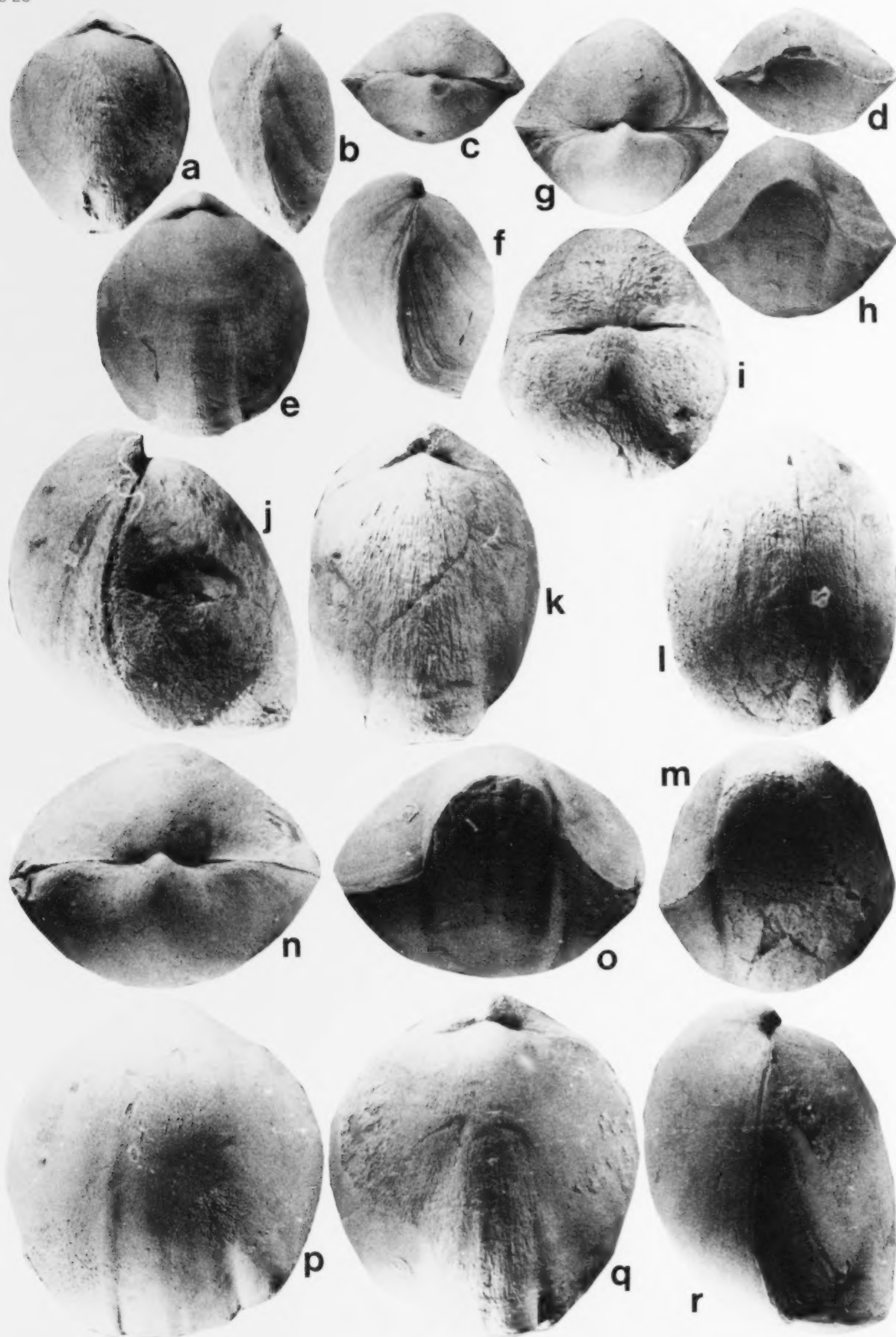


Plate 29

Fig. A, a–s. *Septatrypa petesvika* n. sp.

Petesvik, basal Hemse Formation (W facies), unit 'A', early Ludlow.

a–e. Paratype Br44447, immature shell.

f–j. Holotype, Br59763, well-preserved mature shell with epibionts on dorsal valve posterior and ventral valve anterior fold.

k–n. Immature specimen, paratype Br44446, with pinched anterior fold probably representing shell damage during growth.

o–s. Paratype, larger, gerontic shell, paratype Br44419, with wide fold, central narrow bisulcation, all $\times 2$.

Fig. B, a–i. *Glassia elongata* Davidson, 1881

Farley Mbr., Coalbrookdale Fm., Wenlock.

a–c. Paralectotype BB68828, a mature specimen showing weak bisulcation, Tickwood.

d–f. Paralectotype B34856-1, Farley Dingle, with transapical foramen.

g–i. Paralectotype B34856-2, Farley Dingle, all $\times 3$.

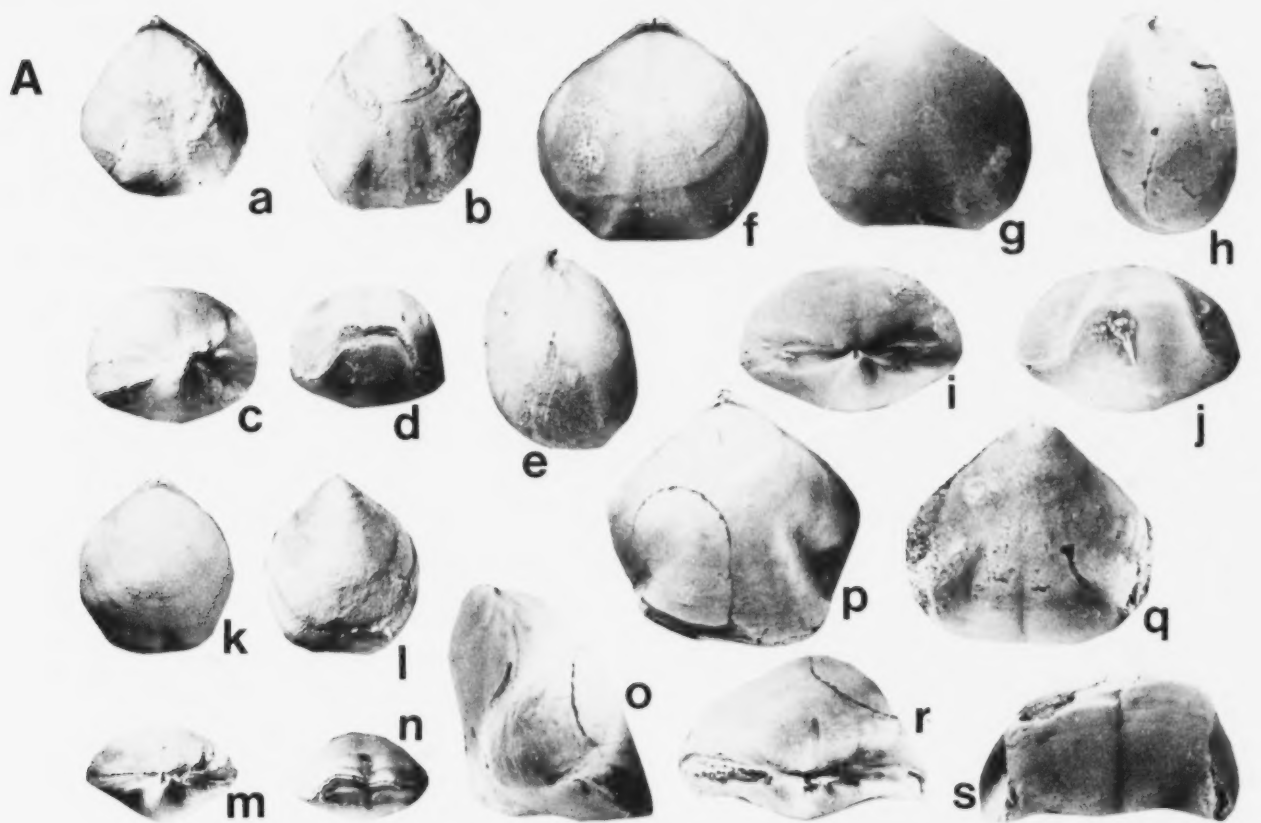
Fig. C, a–m. *Glassia djauvika* n. sp.

Djupviksvägen 1, Mulde Marl, Wenlock.

a–e. Holotype Br106523, well-preserved specimen.

f–j. Paratype Br106524, specimen with prominent bisulcation.

k–m. Specimen with growth lines, Br106577; all, $\times 3$.



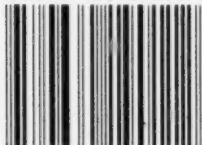


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ISBN 0-660-19011-7



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